"matter" which could not be discovered by the examination of bodies which had never lived.

ue of eri- ntal thod. It would not be a hard task to give chapter and verse for the assertion that the experimental method has, especially in these later times, supplied the chief means of progress in physiology; but it would be a long task, and we may content ourselves with calling attention to what is in many respects a typical case. We referred a short time back to the phenomena of "inhibition." It is not too much to say that the discovery of the inhibitory function of certain nerves marks one of the most important steps in the progress of physiology during the past half-century. The mere attainment of the fact that the stimulation of a nerve might stop action instead of inducing action constituted in itself almost a revolution; and the value of that fact in helping us on the one hand to unravel the tangled puzzles of physiological action and reaction, and on the other hand to push our inquiries into the still more difficult problems of molecular changes, has proved immense. One cannot at the present time take up a physiological memoir covering any large extent of ground without finding some use made of inhibitory processes for the purpose of explaining physiological phenomena.

Now, however skilfully we may read older statements between the lines, no scientific—that is, no exact—knowledge of inhibition was possessed by any physiologist until Weber, by a direct experiment on a living animal, discovered the inhibitory influence of the pneumogastric nerve over the beating of the heart. It was of course previously known that under certain circumstances the beating of the heart might be stopped; but all ideas as to how the stoppage was or might be brought about were vague and uncertain before Weber made his experiment. That experiment gave the clue to an exact knowledge, and it is difficult, if not impossible, to see how the clue could have been gained otherwise than by experiment; other experiments have enabled us to follow up the clue, so that it may with justice be said that all that part of the recent progress of physiology which is due to the introduction of a knowledge of inhibitory processes is the direct result of the experimental method. But the story of our knowledge of inhibition is only one of the innumerable instances of the value of this method. In almost every department of physiology an experiment or a series of experiments has proved a turning-point at which vague nebulous fancies were exchanged for clear decided knowledge, or a starting-point for the introduction of wholly new and startling ideas. And we may venture to repeat that not only must the experimental method be continued, but the progress of physiology will chiefly depend on the increased application of that method. The more involved and abstruse the problems become, the more necessary does it also become that the inquirer should be able to choose his own conditions for the observations he desires to make. Happily, the experimental method itself brings with it in the course of its own development the power of removing the only valid objection to physiological experiments, viz., that in certain cases they involve pain and suffering. For in nearly all experiments pain and suffering are disturbing elements. These disturbing elements the present imperfect methods are often unable to overcome; but their removal will become a more and more pressing necessity in the interests of the experiments themselves, as the science becomes more exact and exacting, and will also become a more and more easy task as the progress of the science makes the investigator more and more master of the organism. In the physiology of the future pain and suffering will be admissible in an experiment only when pain and suffering are themselves the object of inquiry. And such an inquiry will of necessity take a subjective rather than an objective form. (M. F.)

PART II.—NERVOUS SYSTEM.

[By John G. McKendrick.

To supplement the foregoing general sketch some detailed account must be given of the physiology of the several functions. NUTRITION (*q.v.*) has received separate treatment; a sketch of the "Nervous System" is now appended; and RESPIRATION and REPRODUCTION will be dealt with in their places.

However complex may be the anatomical arrangements in man and the higher animals, the nervous system consists essentially of three portions: (1) *central* masses of nervous matter, or *ganglia*, constituting the brain and spinal cord, and containing invariably nerve-cells; (2) *peripheral* or *terminal* arrangements, existing in the organs of sense, in muscle, and in electric organs; and (3) *nerves*, or internuncial cords connecting the central with the peripheral organs. The nerves may be regarded as conductors of a mode of energy which, for want of a better term, is termed "nerve-force," originating either in the nerves themselves on the application of a stimulus or in the terminal organs or in the central organs. Thus, if a nerve be irritated at any point of its course, a change is set up in the nerve-fibres at the point of irritation, and this change is propagated along the nerve-fibres to a central or terminal organ, thus producing a characteristic phenomenon,—it may be a sensation of pain or of pleasure, an involuntary movement, the contraction of a muscle, or a discharge of electricity. Again, the stimulus may act on a terminal organ, such as the retina, setting up a change which is then propagated or conveyed to the brain by the optic nerve, there giving rise to a sensation of light or colour. Finally, the nervous action may originate in a central organ, as is the case when a voluntary movement is made. The voluntary impulse, in this instance, originates in the brain; a change passes along nerve-fibres from the brain to the muscles, and as a result the muscles contract. We have therefore to discuss the general properties and modes of action of nerves, terminal organs, and central organs.

1.—NERVES.

c- of es. *Structure of Nerves.*—A general description of the structure of nerves and of nerve-fibres will be found in vol. i. p. 859 *sq.*; but there are a few points of physiological importance still to be noticed. Two kinds of nerve-fibres exist in the body, white or medullated fibres, so called because each fibre has a sheath indicated by a double contour (see fig. 1), and the pale or non-medullated. The medullated nerve-fibres form the white part of the brain, spinal cord, and nerves. They vary in diameter from the $\frac{1}{1500}$th to the $\frac{1}{12000}$th of an inch, and when of very small size often show varicosities or swellings. Each fibre consists of three parts: (1) an external sheath, or primitive sheath; (2) within this the medullary sheath or white substance of Schwann; and (3) in the centre an axial fibre, the cylinder axis of Purkinje, or band of Remak. The axis-cylinder in a fresh nerve seems to be homogeneous; but with high powers and proper illumination, and more especially by the action of perosmic acid, it is seen to be formed of extremely fine fibrillæ. It is continuous from end to end of the nerve. The medullary sheath shows at certain intervals interruptions called the "nodes of Ranvier" (see fig. 2). In the middle of each internode an oval nucleus is found in the medullary sheath. The pale or non-medullated fibres, sometimes called the "fibres of

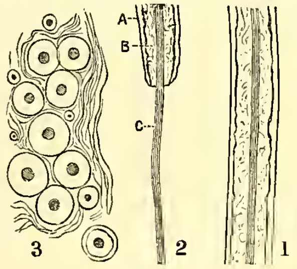

Fig. 1.

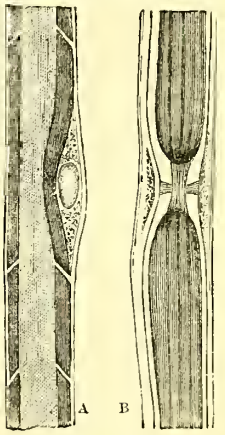

Fig. 2.

FIG. 1.—(1) Medullated nerve-fibres, showing double contour; (2) a similar fibre in which A is primitive membrane, B medullary sheath, C axial cylinder protruding beyond the broken end of the fibre; (3) transverse section through medullated fibres of a nerve showing axial cylinder in each fibre. Between the fibres is the interfibrous connective tissue.

FIG. 2.—Medullated nerve-fibres. A, medullated nerve-fibre, showing subdivision of medullary sheath into cylindrical sections imbricated with their ends; a nerve-corpuscle with an oval nucleus is seen between neurilemma and medullary sheath; B, medullated nerve-fibre at a node or constriction of Ranvier; the axis-cylinder passes uninterruptedly from one segment into the other, but the medullary sheath is interrupted. (Key and Retzius.)

Remak," are found chiefly in branches of the sympathetic nerve. They have no double contour, and they often give off branches which anastomose, a condition never found in the course of medullated nerves. If the axis-cylinder of a nerve-fibre be traced inwards to a nerve-centre it is found to end in the pole or process of a nerve-cell, whilst in the periphery it ends in a terminal organ, in muscle, blood-vessel, gland, skin, or electric organ. It may therefore be presumed that the axis-rod is the conducting and so far the essential constituent of the nerve-fibre.

Chemical constitution.

Chemical Constitution.—Little is known of the chemical constitution of the nerve-fibre. The medullary matter contains fatty substances such as lecithin ($C_{44}H_{90}NPO_9$). The axis-rod appears to contain albuminous substances. Cholesterin ($C_{26}H_{44}O + H_2O$) and creatin ($C_4H_9N_3O_2$) have been obtained from nerves along with a small amount of gelatin and a horny matter, neurokeratin (Hermann). Nerves contain about 30 per cent. of water. Their reaction to test-paper is neutral. Nothing is known regarding the chemical changes occurring in a nerve-fibre during a state of activity, nor of the chemical products formed at that time. It has been stated that a nerve becomes acid after death (Funke).

As to the micro-chemistry of the nervous elements, it may be stated that the axis-cylinder contains an albuminous substance different from myosin; it gives a red colour on boiling with Milton's reagent (an acid nitrate of mercury); it is dissolved in weak solutions of ammonia, caustic potash, and chloride of sodium; it is hardened by solutions of chromic acid, bichromate of potash, and corrosive sublimate; it reduces the chloride of gold; and it shows transverse markings on the action of nitrate of silver. The white substance of Schwann is blackened by perosmic acid and is soluble in alcohol, ether, and oil of turpentine, thus showing its fatty character. The primitive sheath is a substance of a collagenous nature,—that is, it yields gelatin on boiling. According to some, digestion in gastric or pancreatic juice leaves an insoluble matter like that found after the digestion of corneal or epidermic tissues, and hence called "neurokeratin."

Excitability.

Excitability.—The special property of a nerve-fibre is termed "excitability." Every kind of living protoplasmic matter is irritable,—that is, it responds in some way to a stimulus. Thus, if a morsel of protoplasm, such as an amœba or a cartilage-cell or a white blood-corpuscle, be stimulated mechanically or by shocks of electricity, it will contract or change its form. Again, if living muscular fibre be thus stimulated it also will contract. This property of responding to a stimulus is termed "irritability"; and in the structures mentioned the property is manifested by movement as the obvious phenomenon, but it is well known that more obscure phenomena follow the application of the stimulus. In the case of living nerve there is irritability also,—that is, the nerve responds to a stimulus; but in a portion of isolated nerve no change is visible. If, however, the nerve be connected at one end with its appropriate central or terminal organ we may have evidence of something having been transmitted along the nerve. Thus there may be sensation or movement, or both. Nerves are more irritable than contractile matter, and the term "excitability" is applied to the special irritability of nerve. The same strength of stimulus will act more powerfully on a nerve than on a muscle (Rosenthal). The use of the term "property" in physiology does not imply the idea of any kind of inherent force or entity, but simply that, in the case of muscle and nerve, irritation is followed by certain phenomena seen only in living matter.

(1.) The excitability of nerves is affected by certain conditions. Injury to the nerve, the application of caustics, and drying quickly destroy it. When a nerve is divided the excitability is increased for a short time, then rapidly diminishes, and finally disappears near the point of section. The end of the nerve still connected with central organs undergoes these changes in excitability more quickly than the portion cut off. As shown by Augustus Waller, when a nerve is separated from its central organ, such as the grey matter of the spinal cord for the motor roots, and the ganglia on the posterior roots for the sensory roots, the end of the nerve separated from the centre undergoes fatty degeneration. If, however, the cut ends of the nerve be brought into accurate contact, union soon takes place. Surgeons have frequently observed a return of sensibility to a part within a few days after the sensory nerve had been divided and the cut ends again brought into contact. Continued or excessive activity of a nerve soon lowers and may abolish excitability, thus producing exhaustion. On the other hand, a lengthened period of absolute repose lowers excitability, and if the nerve be inactive beyond a certain time it wastes, becomes thinner, and fatty degeneration occurs in its substance. Heat increases, whilst cold diminishes, excitability. In the case of frogs' nerves temperatures above 45° C. destroy excitability the more rapidly as they approach 70°, at which point it is almost instantaneously destroyed. Below 45° a rise of temperature first increases and then diminishes excitability, and it has been observed that whilst increasing its intensity it diminishes its duration (Afanasieff, Hermann). Finally, a diminished supply of blood quickly causes a fall of excitability.

Stimuli of nerves.

(2.) Nerves may be excited by various kinds of stimuli: (*a*) mechanically, as by intermittent pressure, beating, section, pricking, &c.; (*b*) thermally, by variation of temperature; (*c*) chemically, by the application of such substances as acids, alkalis, or metallic salts; (*d*) electrically, by continuous or induced currents; and (*e*) normally, by changes in the central or terminal organs. Mechanical irritation is applied during life when the trunk of a nerve is pressed upon. Radiant heat acts on the nerves of the skin, or heat may be applied by conduction from a hot body in contact with the surface. Little is known as to the specific effects of heat on the nerves of the human being. In the frog it has been found that a temperature of from 34° to 45° C. stimulates the motor nerves; about 40° C. sudden alterations of temperature may cause twitching of the connected muscles (Hermann). Many chemical substances in sufficient concentration will quickly destroy a nerve; but if they are in weak solutions the result may be stimulation. Thus, concentrated solutions of the mineral acids, alkalis, alkaline salts, concentrated lactic acid, and concentrated glycerin may act as strong stimulants (Kühne).

(3.) The influence of electrical stimulation of nerves demands more elaborate description. The effects, as already indicated, can be observed only when the nerve is connected with a muscle or with a central organ. In the first case electrical stimulation is followed by contraction of the muscle, in the second by a sensation if the central organ is the brain. Consequently we have to consider the phenomena following electrical stimulation (*a*) of a motor nerve and (*b*) of a sensory nerve.

Electrical stimul tion o motor nerve.

(*a.*) *Electrical Stimulation of a Motor Nerve.*—A perfectly constant current of electricity, of moderate quantity and intensity, flowing through a portion of nerve produces no evident effect on the muscle, but any variation in the intensity or density of the current causes irritation, and the muscle gives a twitch. The effect is most apparent when the current is allowed to flow into the nerve and when it is suddenly cut off, or, in other words, at the moment of opening and of closing the circuit. The rapidity with which the variation in the density of the current is effected also has an important influence. Thus the shocks of frictional electricity stimulate strongly, because, although the amount of electricity is small, the currents are extremely rapid in appearing and disappearing. In like manner the quick shocks from induction-coils produced by rapidly opening and closing the primary circuit are strongly stimulating. Again, a very powerful current may pass through a nerve without exciting it, if it pass gradually. Occasionally a very weak current sent through a portion of nerve will cause a contraction, whilst a very strong current may fail to do so. In fact, the phenomenon of contraction of a muscle is influenced (α) by the direction and (β) by the strength of the current sent through the nerve. When the current is transmitted from the muscle in the direction of the spinal cord it is called an "upward" or "centripetal" current, when from the cord in the direction of the muscle it is called a "downward" or "centrifugal" current. Its strength is graduated by employing small Grove's cells, one cell giving a weak current, two or three giving a medium current, and four to six or seven a strong current. To graduate its amount more precisely resistance-coils may be introduced into the circuit, or we may employ a rheochord, by which a portion of the current is shunted back to the battery, whilst the remainder is allowed to pass to the nerve. In the circuit a key or interrupter is interposed, and so arranged that when the key is opened the current is broken or interrupted, and when the key is closed the circuit is completed and the current passes to the nerve. With these arrangements, and employing the sciatic nerve of a frog attached to the limb, the following results are readily obtained.

Current Strength.	*Key.*	*Upward Current.*	*Downward Current.*
Weak.	Close.	Contraction.	Contraction.
Weak.	Open.	Rest.	Rest.
Medium.	Close.	Strong contraction.	Strong contraction.
Medium.	Open.	Strong contraction.	Strong contraction.
Strong.	Close.	Rest.	Rest.
Strong.	Open.	Very strong contraction.	Contraction.

That is to say, on beginning with a very feeble current neither opening nor closing causes a contraction, but on strengthening it up to a certain point contraction appears first on closing, whilst opening produces no effect. By increasing the strength of the current a contraction is obtained both on opening and on closing the key, and by and by, when a certain strength of current is reached, the closing contraction becomes weaker and finally disappears, leaving only a contraction on opening the key. Thus the effects of a strong current are usually the reverse of those caused by a weak current. These facts, usually included under the term "Pflüger's Law of Contraction," have been specially investigated by Pflüger, and the following is the explanation offered by him and generally accepted by physiologists.

Suppose that the sciatic nerve of a frog connected with the isolated limb is stretched over two wires passing from the positive and negative poles of a combination of Grove's elements, with the distance of an inch and a half between the wires. If a key be interposed in the circuit a current will thus pass along one and a half inches of nerve when the key is closed, and be cut off when the key is opened. By having also a commutator or reverser in the circuit we can send the current up or down the nerve at pleasure. Arrangements can also be made for irritating the nerve by another couple of wires coming from an induction-machine, either near the negative or near the positive pole of the current coming from the Grove's elements. It will then be found that near the negative pole the excitability of the nerve is increased, whilst near the positive pole it is diminished,—that is to say, a stimulus from the induction-coil, not sufficient to excite the nerve so much as to cause a muscular contraction if applied near the positive pole, will at once do so if applied near the negative pole; or, a stimulus so strong as to cause tetanus in the muscle when applied near the negative pole may produce no effect when applied near the positive pole. In other words, the nerve near the negative pole is more excitable than in the normal state, whilst near the positive pole it is less so, indicating that at least one of the physiological properties of the nerve has been changed by the action of the continuous current. But a nerve-fibre has also the property of conducting the effects of an impression, or the nerve-force travels with a certain velocity along a nerve, as will be shown lower down. It has been ascertained that near the negative pole the rate of conductivity is increased, whilst near the positive pole it is diminished. Finally, a piece of living nerve, when connected with the terminals of a galvanometer, so that the one terminal touches the surface whilst the other touches the transverse section of the nerve, shows the existence of a current of electricity travelling from the surface of the nerve through the galvanometer to the transverse section,—that is, the surface is positive to the transverse section. This condition is also modified by the transmission through the nerve of a continuous current, so that the difference of potential is increased near the positive pole and diminished near the negative. These results are thus summed up.

State of Nerve.	Functions of Nerve.		
	Electromotive force.	*Conductivity.*	*Excitability.*
Near positive pole	Increased	Diminished	Diminished
Near negative pole	Diminished	Increased	Increased

The properties of the nerve, therefore, are altered by the passage through it of a continuous current, and the altered condition is termed the "electrotonic state," the condition in the neighbourhood of the positive pole, or anode, being termed "anelectrotonic," whilst that near the negative pole or katode is called "katelectrotonic." A certain portion of nerve near each pole is thrown during the passage of a continuous current into these conditions of anelectrotonus and of katelectrotonus, whilst the amount of nerve thrown into the one condition or the other depends on the strength of the current. Further, there is always between the two poles a point of indifference, in which the properties of the nerve seem to be unaltered, and the position of this point depends on the strength of the current. Thus, with a current of medium strength the point is midway between the poles; with a weak current the point is near the positive pole,—that is, a large portion of the nerve near the negative pole is in the katelectrotonic state in which the excitability is increased; and with a strong current the point is near the negative pole,—that is, a large portion of the nerve near the positive pole is in the anelectrotonic state in which the excitability is diminished. Now, according to Pflüger, the stimulating effect of closing the current occurs at the katode only, whilst the stimulating effect of opening the current occurs at the anode only, or a nerve is stimulated by a current on the appearance or increase of katelectrotonus, on closing the circuit, or by the disappearance or diminution of anelectrotonus on opening the circuit. If we suppose that this depends on the modification of excitability near the negative pole, by the molecules of the nerve becoming more mobile, the matter is intelligible. Thus the passage of the molecules from the normal stable condition to the katelectrotonic less stable condition acts as a stimulus, whilst the passage backwards has no effect. On the other hand, the passage from the more stable condition in anelectrotonus to the normal stable condition acts as a stimulus, whilst, again, the reverse action has no effect. This explains why it is that a weak current gives contraction on closing, because on closing a large portion of the nerve near the negative pole passes from the normal into the katelectrotonic state, and this acts as a stimulus. On the other hand, a strong current causes contraction on opening, because on opening a large portion of nerve near the positive pole passes back from the anelectrotonic state into the normal state, and this acts as a stimulus. Again, with currents of medium strength, as both states are equally produced, there is contraction both on opening and on closing. Thus Pflüger's theory accounts for most of the facts; but its weak point is that no reason can be given why a nerve is stimulated only by the appearance of katelectrotonus and by the disappearance of anelectrotonus. It remains only to add that currents passing transversely through nerves produce no stimulating effect. In ascending currents the shorter the piece of nerve between the electrodes the greater the stimulating effect, whereas in descending currents the reverse holds good (Hermann).

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(*b.*) *Electrical Stimulation of Sensory Nerves.*—The effect of stimulating sensory nerves as distinguished from the direct stimulation of sensory or terminal organs has not been sufficiently studied, but, so far as is known, the laws seem to be the same as those relating to motor nerves. When a sensory nerve is stimulated the test must be the resulting sensation. As stimulation of the motor nerve in the condition of anelectrotonus or of katelectrotonus may or may not be followed by a contraction, so stimulation of the sensory nerve may or may not be followed by a sensation, or the character of the sensation may vary just as the muscular contraction may be weak or strong. Further, Donders has shown that electrical stimulation of the vagi or pneumogastric nerves is attended by analogous phenomena, so far as the movements of the heart are concerned. In this case, however, as will be shown lower down in discussing the phenomena of nervous inhibition, the result is not movement but arrest of movement.

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(*c.*) *Chauveau's Researches on Unipolar Excitation.*—Chauveau has studied the comparative influence of the two poles of any arrangement supplying a continuous current,—that is, he has tried the stimulating effect, supposing either the positive or the negative pole be applied to the nerve whilst the other is in contact with another part of the body. He has found, amongst other more abstruse and less practical results, that there is in each case a certain intensity of current corresponding to the physiological condition of the nerve by which the influence of one pole is the same as that of the other. If the intensity of the current be below this medium strength the effect of the negative pole on motor nerves is greater than that of the positive; but, if the intensity be above, the reverse is the case,—that is, the positive pole is the stronger excitant. In the case of sensory nerves Chauveau found that application of the negative pole with a moderately strong current was more painful than application of the positive pole. Thus the influence of unipolar excitation with a strong current on motor nerves is the reverse of that on sensory nerves,—that is, the positive pole is the more powerful on motor nerves, the negative pole on sensory nerves.

Production of tetanus.

(*d.*) *Production of Tetanus.*—Tetanus or cramp of a muscle is produced when its nerve is stimulated by successive irritations at intervals so short that the muscle has no time to relax between them, and consequently it passes into a state of more or less firm contraction. A single muscular contraction may be called a twitch of the muscle, but in tetanus or cramp the individual contractions are fused together so as to maintain a rigid state of the muscle for some time. A rapid series of induction shocks, each of short duration, always produces tetanus, even if they are sent to the muscle at the rate of 15 per second. A continuous current, on the other hand, usually causes contraction only at the moment of opening and closing the circuit, but occasionally tetanus may be seen *during* the passage of the current. Tetanus during the passage of a constant current has been attributed to electrolytic changes in the nerve. Pflüger holds that this is a normal production of tetanus and may be seen even with feeble currents; but certainly it is very difficult to demonstrate. Long ago Ritter showed that, if a constant current of sufficient intensity be sent up a nerve for a considerable time, say half an hour, and then be suddenly interrupted, tetanus lasting for eight or ten seconds may be seen, which disappears on again closing the current. Ritter's tetanus, according to Pflüger, is really due to the stimulation caused by the disappearance of anelectrotonus, which occurs, as we have seen, when the current is opened, and the proof he offers is that the tetanus disappears when the muscle is cut off from the anelectrotonic portion. Tetanus may also be caused by the mechanical irritation of the nerve, or by heat, or by chemical substances.

Nervous conductivity.

Nervous Conductivity.—When a nerve is irritated at any point in its course a change is produced which is propagated along the nerve,—that is, the nerve conducts, and the phenomenon is called the "nerve-current." The velocity of transmission can be measured only by the use of delicate apparatus, as the time occupied is too short to directly affect consciousness. For example, when the tip of the finger is touched the mind apparently perceives the contact without any loss of time. But it can be shown that an appreciable interval of time elapses between the instant the finger is touched and the instant the mind perceives the impression. During this time a change passes along the nerve from the point touched to the brain. The method usually employed for determining the velocity of the nerve-current consists in preparing the gastrocnemius muscle of a frog with the sciatic nerve attached, and connecting it with a recording apparatus, so that if the muscle be caused to contract by irritating the nerve the record of the contraction may be made on a rapidly-moving surface. If, then, the nerve be irritated in two consecutive experiments, first close to the muscle, and secondly at a distance from it, and the muscle be caused to contract in each case, it will be found that it does not contract so soon when the nerve is irritated at a distance from the muscle as when it is irritated close to it; in other words, if the nerve be irritated at a distance from the muscle the transmission of the nervous impression from the point irritated to the muscle occupies an appreciable time. If, then, we know the length of nerve between the two points irritated, we can determine the length of time the nerve-current took in passing along that distance of nerve.

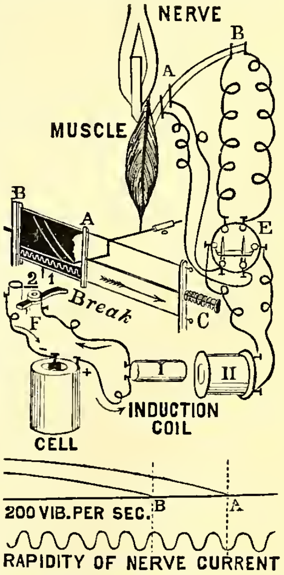

Fig. 3.—Diagram showing arrangement of apparatus in measuring rapidity of nerve-current.

Measurement of velocity in nerves.

(1.) *Measurement of Velocity in Motor Nerves.*—Many ingenious methods have been devised for this purpose, but the simplest is the use of the "spring myographion" of Du Bois-Reymond (see fig. 3). The apparatus consists of a smoked-glass plate, which is driven in front of the recording stylet of the myograph by the recoil of a steel spring C. Underneath the frame carrying the glass plate are two binding screws 1 and 2, to one of which is attached a rectangular arm of brass 1, which can so move horizontally as to establish metallic connexion between the two binding screws (marked *Break*, F). By means of these binding screws the myograph is interposed in the circuit of a galvanic element and the primary coil I of an induction-machine, and the brass arm is so placed as to connect both binding screws, thus completing the circuit. From underneath the frame carrying the smoked-glass plate there descends a small flange, which (when the glass plate, by releasing a catch not seen in the figure, but close to C, is driven across by the spiral spring from left to right) pushes the brass arm aside and thus interrupts the circuit of the primary coil. When this occurs an opening shock is transmitted from the secondary coil II to a commutator E, an instrument by which electric currents may be transmitted to the nerve either at a point close to the muscle at A, or at a distance from it at B. Suppose the apparatus all arranged so as to send the shock to the nerve at a point close to the muscle A, the muscle stimulated contracts, and draws by means of the stylet, on the smoked surface of the glass, the curve seen in the lower part of it at A. This leaves the horizontal line (which would be drawn by the stylet were the muscle at rest) at A. Arrangements are then made for another experiment, in which the nerve will be stimulated at a distance from the muscle, at the point B in the upper part of the diagram. This is done by again placing the smoked-glass plate in proper position, closing the primary circuit by the brass arm at the binding screws, as already described, and reversing the commutator so as to send the shock along the wires to B. The muscle again contracts when the primary circuit is opened, and this time it describes on the smoked surface the curve B, seen to the left of the curve A. It will be perceived that this curve leaves the horizontal line at B,—that is, a little *later* than when the nerve was stimulated close to the muscle. It follows, therefore, that the distance on the horizontal line from A to B represents the time occupied by the transmission of the nervous impulse from B to A of the nerve. With suitable arrangements, the rate of movement of the glass plate can be measured by bringing into contact with it a marker on one of the prongs of a vibrating tuning-fork. The waves thus recorded enable the experimenter to measure with accuracy the rate of movement of the glass plate, and consequently the minute interval of time between A and B. In the diagram it will be observed that there are $2\frac{1}{2}$ waves between A and B; each represents $\frac{1}{200}$th of a second; therefore the $\frac{1}{80}$th of a second is the time represented by the distance A, B; or, in other words, the $\frac{1}{80}$th of a second was occupied by the nerve-current in passing along the portion of nerve from B to A.

(2.) *Measurement of Velocity in Sensory Nerves.*—Suppose a sensory nerve to be excited in the hand; the theory of nervous conduction is that a change is propagated along the nerve to the brain, and that in the brain the molecular changes occur which result in a sensation. The individual having the sensation may feel it and make no sign by which any one else might be made aware that he has felt it, or the subject of the sensation might, by a muscular movement, such as the motion of an arm, let any one else see that he has felt the sensation. We have no means of knowing whether or not an individual has felt a sensation except by the individual making some kind of gesture or muscular movement. Now it is clear that, if we regard the brain as the seat of the changes resulting in sensation, the nearer any stimulated portion of skin is to the brain the sooner will the brain feel and respond to the stimulus. Thus, if the skin on the big toe of the right foot be stimulated, the effect of the stimulus passes to the brain and there calls forth a sensation, but if the stimulus be applied to the skin at the top of the thigh it is evident the effect has to pass along a shorter length of nerve and that the sensation in the brain will be aroused sooner. If we suppose that in each case the individual who is the subject of the experiment indicates the moment he feels the sensation, and that the instant the stimulus is applied successively to the skin on the toe and on the thigh is also accurately recorded, it is clear that he will signal the sensation of stimulation of the toe a little later than when he signals stimulation of the skin on the thigh, and that the difference will indicate the time required by the change in the nerve to pass along the length of nerve from the toe to the thigh. In the observation it is assumed that the time required for the changes in the brain resulting in sensation and volition, for the transmission along the motor nerve, and for the muscular contraction required to signal is the same in each experiment. Thus, supposing the total time between the moment of stimulating to the moment when the signal that the sensation has been felt and responded to is x, it is clear that this time is composed of a, the time required for the passage of the nerve-current in the first experiment from the toe to the brain, of b, the time required for the changes in the brain involved in sensation and volition, and of c, the time required for the transmission along the motor nerves and for the muscular contraction to move the signal,—that is, $x=a+b+c$. But, if the time between the moment of stimulating the thigh to the moment of signalling be shorter, and supposing that b and c are constant, then a varies according to the length of the nerve. Suppose the difference of time between the registration of stimulating at the toe and at the thigh to be y, then in the second experiment $x=a-y+b+c$,—that is, y= the time occupied by the passage of the nerve-current from the toe to the thigh. This method has also been used to measure the time required for signalling a nervous impression in various circumstances, or what is usually called the "reaction period." The most convenient apparatus for the purpose is a chronograph made by König of Paris, the instrument being fully described in M'Kendrick's *Outlines of Physiology*, pp. 538-542.

The general result of measurements made by these methods is that the nerve-current travels slowly compared with the velocity of electricity or of light. In the motor nerves of the frog the velocity is about 87 feet (26 to 27 metres) per second, and in man and warm-blooded animals somewhat faster, 115 to 130 feet (35 to 40 metres) per second. The results as to velocity in sensory nerves vary from 50 to 100 metres per second. Cold retards, heat accelerates, the velocity. As already stated, the velocity is also retarded in a nerve in an anelectrotonic, and accelerated in a katelectrotonic state. The remarkable point is that the transmission of the nerve-current is slow, and that events appearing to our consciousness instantaneous require a considerable time for their occurrence. It may be laid down as a general truth that all kinds of nervous actions, even those considered as purely psychical, require time.

Heat-production by nerves.

Production of Heat by Nerves.—It is extremely doubtful whether the production of heat by a nerve in action has been detected, although theoretically one would expect heat to be so produced. Schiff observed an increase of temperature on tetanization in the nerves of warm-blooded animals that had been artificially cooled; on the other hand, Helmholtz and Heidenhain's experiments yielded only negative results.

Electrical Phenomena of Nerve.—When a piece of nerve is properly brought into contact with the terminals of a sensitive galvanometer, a current flows through the galvanometer from the surface of the nerve to its transverse section (see fig. 4).

If metallic conductors, composed (say) of zinc, from the galvanometer were brought into connexion with a piece of nerve removed from an animal newly killed, little or no current would be obtained, and even if there were a current it might be due to contact of the metallic conductors with the living tissue exciting electrolytic decomposition. Hence it is necessary to have a fluid interposed between the metal and the animal tissue, say, for example, the zinc wire or plate forming the terminals of the galvanometer is immersed in a saturated solution of sulphate of zinc. But as sulphate of zinc solution would have the effect of irritating the living muscle it is necessary to have an inactive substance between the tissue and the sulphate of zinc solution. All these conditions are fulfilled by the non-polarizable electrodes of Du Bois-Reymond, of which there are various forms. Two zinc troughs, mounted on insulating plates of vulcanite, have the inner surfaces carefully amalgamated. These are filled with a saturated solution of sulphate of zinc, and in each trough is placed a small cushion of clean blotting or filter paper, which quickly becomes permeated with the solution. Finally, a small plate of sculptor's clay, or kaolin, moistened with a half per cent. solution of common salt, or, still better, with saliva, is laid on each paper pad. These clay pads are for guarding the tissue from the irritant action of the sulphate of zinc. Wires are carried from the troughs to the galvanometer, and a key is interposed in the circuit. The object of these careful arrangements is to secure that no current is formed by the apparatus itself. If now a small piece of nerve be so placed on the clay pads that the transverse section touches one pad and the longitudinal surface the other, and the key is opened, a current passes through the galvanometer, as indicated by the swing of the needle. Suppose that the needle is allowed to come to rest, the amount of deflexion of course indicating the strength of the current, and the nerve is now irritated so as to call forth its physiological activity, then the needle swings back towards zero. This backward swing is called the negative variation of the nerve-current. The electromotive force of the current obtainable from a frog's sciatic nerve is about ·022 of a volt, and somewhat more from the sciatic nerve of a rabbit. This is somewhat less than the electromotive force of a frog's muscle, which varies from ·035 to ·075 of a volt. According to the views of Hermann, the negative variation-current is a true current indicating, and indeed preceding, the physiological activity of the nerve. He denies that the currents pre-exist in nerve or muscle, and states that the first current observed when the nerve is laid on the pads is simply due to the lower potential of the transverse section, caused by the rapid death of the nerve-substance. The nerve-current excited by a series of irritations, say feeble induction-currents, may be regarded as composed of a wave-like series of momentary currents, each of which is preceded by a negative variation-current. Thus the electrical phenomena of nerve are similar in kind to those manifested by living muscle.

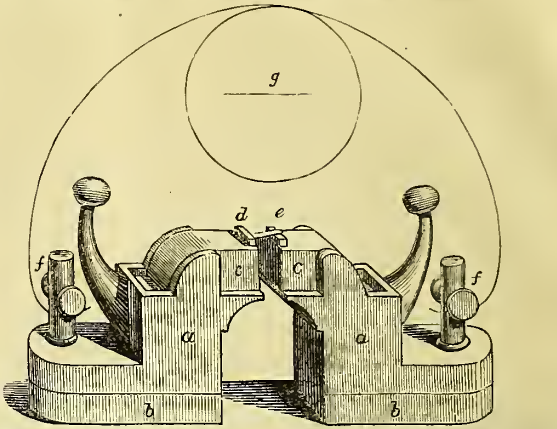

Fig. 4.—Diagram of apparatus of Du Bois-Reymond for experiments on electrical condition of muscle and nerve. *a*, zinc troughs, mounted on pieces of vulcanite *b*; *c*, paper pads; *d*, *e*, small pieces of moist clay; *f*, *f*, binding screws for attaching terminals of galvanometer *g*. A small piece of paper connects *d* and *e*, and thus completes the galvanometer circuit. (Wundt.)

Nutrition of nerves.

Nutrition of Nerves.—Probably nerves are nourished by the plasma reaching the axis-cylinder at the nodes of Ranvier; but it would appear from the researches of Waller that the nutrition of the nerve-fibre is influenced by the nerve-cell with which it is connected. The so-called "law of Waller" is well illustrated in the case of division of the roots of the spinal nerves. Each of these nerves has two roots,—a posterior, sensory, on which there is a ganglion; and an anterior, motor. If the anterior root be divided, in the course of a few days the end of the nerve cut off from the spinal cord is found to be undergoing degeneration, whilst the end attached to the cord is still normal. Again, if the posterior root be divided between the ganglion and the cord, the end remaining in connexion with the ganglion remains unaffected, whilst the other end undergoes degeneration. This degeneration, in the case of a motor nerve, affects the nerve to its very terminations. The axis-cylinder disintegrates into drops of fatty matter, and the medullated structure entirely disappears. It is well known that when a nerve is cut the ends may reunite so completely as to ensure a return of the normal function in from two to five weeks. According to Ranvier, the axis-cylinders in connexion with the central portion play an important part in this regeneration. They become larger, striated, and by and by form new axis-cylinders, which pass into the cicatricial tissue and come into contact with the other end of the divided nerve. This is a remarkable confirmation of the view of Waller that the nutritional activity of a nerve-fibre is in the direction of its physiological activity.

Nerve-currents.

Nature of Nerve-currents.—The intrinsic nature of the change in a nerve-fibre effected by a stimulus is quite unknown; but it is important to appreciate clearly the view that a nerve is both a receiver and a conductor of impressions. It can be stimulated in any part of its course, and from the stimulated point some kind of change is propagated along the nerve. This change is analogous to the passage of electricity along a conductor, or to the rapid passage onwards of a series of chemical decompositions, as when a long thin band of gun-cotton properly prepared is seen to slowly burn from end to end, or to the quick transmission of isomeric changes; but the analogy is not complete in any case. Whatever the change may be, however, it does not appear to pass from one nerve-fibre to another running alongside of it. Each fibre conducts only its own impression, and there is nothing analogous to the inductive effect of one electrical conductor upon an adjacent one. Another question much debated is whether sensory and motor nerves act in the same way; or, in other words, is there any essential difference between them? There appears to be no difference in mode of action; the difference in the effect produced depends on the apparatus in which the nerve ends. Thus there may be contraction of a muscle if the nerve terminates in a muscle, change of the calibre of a blood-vessel if the nerve ends in that structure, secretion from a gland if the nerve is in connexion either with the vessel or the nerve-cells of a gland, an electrical discharge if the nerve ends in the electrical organ of a *Torpedo* or *Gymnotus*, and a feeling or sensation if the nerve-fibres go to a sentient brain. In all these instances the nature of the change in the nerve and the mode of its transmission are the same, and the results are different because the nerves terminate in different kinds of structure. It would appear from experimental evidence that, when a nerve-fibre is irritated, say about the middle of its length, a change is simultaneously propagated towards each end; but, as only one end is in connexion with an apparatus capable of responding, the effect at this end is the only one observed. Thus, if a motor nerve be irritated, there is muscular contraction, in consequence of the stimulus rousing the muscular substance into activity, probably through the agency of the end-plates; but there will be at the same time a backward wave along the nerve to the motor centres in the cord or brain. It is doubtful whether the nerve-energy becomes weaker or gathers intensity as it passes along a nerve; but the balance of evidence is in favour of the view that the so-called "avalanche theory" of Pflüger, according to which the energy gathers intensity as it passes along, is incorrect.

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Classification of Nerves.—Functionally, nerves may be classified into motor, sensory, vascular, secretory, and inhibitory. The original meaning attached to the term "motor" nerve was a nerve entirely composed of fibres by the excitation of which influences were conveyed to a muscle which caused the muscle to contract. As these influences passed outwards from a nerve-centre towards the periphery of the body they were also termed "efferent" nerves. On the other hand, nerves were found which, when stimulated, gave rise to sensations of pleasure or of pain, and these were called "sensory" nerves. Finally, it was shown that a third class of nerves were composed both of sensory and of motor fibres, and they were called "senso-motor" nerves. Sensory nerves were also subdivided into those of general and those of special sensibility. This was an artificial classification based on the fact that when a nerve of so-called special sensibility, such as the optic, was stimulated in any way the same kind of sensation followed. Thus stimulation of the optic nerve by cutting, pricking, pressure, or electricity is always followed by a luminous sensation. But the progress of research showed that when certain nerve-fibres were stimulated the result was not necessarily a muscular contraction: it might be contraction of a blood-vessel, modified secretion of a gland, or a diminution or arrest of some kind of nervous action. These facts demand another classification of nerves such as the following.

- CENTRIFUGAL, or EFFERENT, or MOTOR, conveying influences outwards from a nerve-centre.
  1. *Motor*, sometimes termed *efferent*, to muscles, exciting contraction.
  2. *Secretory*, to the cells of glands, causing secretion, possibly a particular kind of secretion.
  3. *Vascular*, or *vaso-motor*, to the walls of blood-vessels, so as to cause contraction (*vaso-motor*) or dilatation (*vaso-dilators*, or *vaso-inhibitors*).
  4. *Inhibitory*, so affecting other centres of nervous activity as to moderate or neutralize their action.
  5. *Electrical*, so affecting a special organ as to call forth electrical discharges, as in electric fishes, *Torpedo*, *Gymnotus*, *Malapterurus*, &c.
- CENTRIPETAL, or AFFERENT, or SENSORY, conveying influences inwards towards a nerve-centre.
  1. *Sensory*, causing more or less acute sensations.
     - a. *General*, conveying to nerve-centres in brain influences which cause sensations of a vague character, scarcely perceptible to consciousness, and not permanent, as from lungs, heart, stomach, &c.
     - b. *Special*, conveying to nerve-centres in brain influences which cause visual, auditory, gustatory, olfactory, or tactile sensations.
  2. *Afferent*, or *reflex*, conveying to nerve-centres influences which usually cause no sensation, and which may or may not be followed by movements, secretions, changes in calibre of vessels, &c.

In addition there are nerve-fibres connecting nerve-cells in the great centres, to which no special functions can be attributed.

2.—TERMINAL ORGANS.

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Although, as has been shown, a nerve may be stimulated in any part of its course, the stimulus is usually applied to a special structure adapted physiologically for the reception of the particular kind of stimulus. Such a special structure may be termed a "terminal organ." For example, in the mechanism of vision (see EYE, vol. viii. p. 821 *sq.*) there are the retina or terminal organ, the optic nerve or conductor, and the brain or a portion of it, the recipient of the impression. The fibres of the optic nerve are not affected by light, but when they are mechanically or electrically irritated the result is a luminous sensation, because the action of the fibres of the optic nerve is to call forth in the brain the mechanism connected with luminous sensations. But light has a specific action on the retina, and in turn the activity of the retina stimulates the fibres of the optic nerve. The retina is therefore the terminal organ adapted for the reception of rays of light. In like manner, each sense has its appropriate terminal apparatus, and these are described under the headings of the various senses, EAR, EYE, SMELL, TASTE, TOUCH. To understand the true nature of nervous action it is necessary to be clear as to the functions of the terminal organs. They are liberating mechanisms. They do not transform the outer energy into the physiological energy, nervous action; but they call it into action. Thus light acting on the retina is not directly transformed into nervous energy, but it excites changes in the retina, which in turn produce activity of the optic nerve. The structure of each of these terminal organs need not be here described, but it may be stated that they all essentially consist of modified epithelium-cells, or what may be called "nerve-epithelium." In tracing their development throughout the animal kingdom it will be found that the simplest terminal organs are epithelium-cells on the surface of the body; but during evolutionary progress from lower to higher forms these cells become more and more modified and more and more protected by descending deeper into the structure of the animal, until we meet with the complicated organs of special sense in the higher animals. Another class of terminal organs is that comprehending the forms at the ends of motor nerves. Such are the end-plates found in muscle, and described in vol. i. pp. 861, 862. The different modes of nerve-termination may be here briefly classified.

Organ.	*Terminal Organ.*	*Effect.*
Skin (see TOUCH)	Tactile cells of Merkel, in the epidermis. Tactile corpuscles of Wagner and Meissner, in papillæ of the skin. End-bulbs of Krause, in conjunctiva, penis, and clitoris. Pacinian bodies, attached to nerves of hand or foot, or in the mesentery. Corpuscles of Grandry, found in bills of birds. Network of fibres, as in cornea.	Touch, pressure, or temperature.
Ear (see vol. i. p. 894, and vol. vii. p. 591).	Hair-cells, supported by arches of Corti, and connected with the basilar membrane.	Hearing.
Eye (see vol. i. pp. 886 and 888, and vol. viii. p. 816).	Rods and cones of retina........	Vision.
Nose (see SMELL)	Rods and olfactory cells........	Smell.
Tongue (see TASTE) ..	Taste-buds and gustatory cells..	Taste.
Muscles (vol. i. p. 862)	Motorial end-plates of Doyère, Kühne, Krause, Ranvier, &c.	Motion.
Glands	Nerve-endings in secreting cells —Pflüger and Kupffer.	Secretion.
Electric organs (see vol. xii. pp. 649, 650).	Laminæ with free cilia-like processes.	Electric discharge.

3.—CENTRAL ORGANS.

A.—General Physiology of Central Organs.

General Structure.—The central organs consist of a special kind of cells called "nerve-cells," of nerve-fibres, both medullated and non-medullated, and of a variety of connective tissue, termed "neuroglia." On cutting into any central nervous organ, such as the spinal cord or brain, two kinds of nervous matter are seen, the white and the grey. The grey consists of nerve-cells, nerve-fibres, and neuroglia, whilst the white is composed chiefly of nerve-fibres with a small amount of neuroglia and no nerve-cells. Nerve cells vary much in form, as will be seen by referring to fig. 5. They may be spheroidal, ovoidal, or irregularly triangular. The cells of the spinal ganglia are usually rounded; those of the sympathetic more angular; those of the spinal cord multipolar,—that is, having many processes or poles connected with them; those of the cerebrum triangular or pyramidal; and those of the cere-

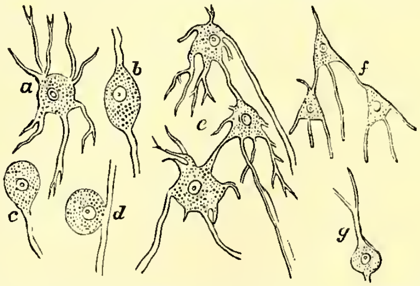

FIG. 5.—Various forms of nerve-cells. *a*, *multipolar*, from grey matter of spinal cord; *b*, *d*, *bipolar*, from ganglia on posterior roots of spinal nerves; *c*, *g*, *unipolar*, from cerebellum; *g* shows indications of a process coming off at lower end; *e*, union of three multipolar cells in spinal cord; *f*, union of three tripolar cells in grey matter of cerebral hemispheres.

Shapes of nerve-cells.

bellum flask-shaped, having processes at each end. A nerve-cell shows a large clear nucleus and a small nucleolus, whilst the cell-substance is very granular. Some observers think they have traced into the substance of the cell a fibrillated structure from the axis-cylinder of the nerve-fibre ending in the pole or process; but this is doubtful, and the appearance may be accounted for by the action of the reagent employed and by the great difficulty of correctly interpreting optical appearances under very high powers. The neuroglia is a delicate interstitial connective substance having small connective-tissue corpuscles imbedded in it.

Chemical substances in nervous matter.

Chemical Constitution of Grey and White Matter.—This is still imperfectly known, and throws almost no light on the functions of the central organs. By various chemical processes the following substances have been obtained from nervous matter: cerebrin, lecithin, albumin, neurokeratin, cholesterin and fats, creatin, xanthin, hypoxanthin, inosite, lactic acid, volatile fatty acids, salts, and water. The grey matter of the brain is distinguished chemically from the white chiefly by containing more water, albumin, lecithin, and lactic acid, and less cholesterin, fat, and protagon (Hermann). Doubtless many of these substances are derived from the disintegration of a more complex chemical substance not yet isolated in a pure state from nervous matter. Petrowsky gives the composition of grey and white matter as follows.

	Grey matter.	White matter.
Water	81·6	68·4
Solids	18·4	31·6
The solids consist of—		
Albumins and gelatin	55·4	27·7
Lecithin	17·2	9·9
Cholesterin and fats	18·7	51·9
Cerebrin	0·5	9·5
Substances soluble in ether	6·7	3·3
Salts	1·5	0·6

The salts found in nervous matter are similar to those in blood, and it would appear that phosphates, or rather combinations in which phosphorus exists, are the most prominent products of analysis. Thus about 40 per cent. of the salts consist of phosphates of soda and of potash—that is, the ash, on analysis, gives this result; but it must not be inferred that in nervous tissue phosphates of the alkalis exist to this amount, as there is every reason to think that phosphorous compounds, along with alkalis, exist in nervous matter, although not in the form usually called phosphates. The remarkably large amount of water, amounting to no less than from 70 to 80 per cent., indicates matter in a condition suitable for rapid molecular changes, on which, no doubt, the functions of the tissue depend.

Excitability and blood-supply.

Excitability of Grey Matter.—As grey matter contains both nerve-fibres and nerve-cells, and as these cannot be separated in any experiment, it is clear that no precise results can be obtained from any effort to distinguish the excitability of grey matter from that of white. The excitability of the grey matter must depend on blood-supply and on the rapid removal of waste-products. If the first be deficient either in quantity or quality, or if the second be not carried on so rapidly as to get rid of the waste-products as they are formed, the activity of the nerve-cells must suffer. The sudden deprivation of blood, as when the heart ceases to beat for even half a second, will cause unconsciousness; the mixture with the blood of a small quantity of bromide of potassium, or of alcohol, or of chloroform or other anæsthetic, or of morphia, will affect the activity of the brain. And it is well known that, when disease of the kidney, or such a disease as an acute fever, affects the body, matters may accumulate in the blood which so contaminate it as to make it unfit to carry on the vital changes on which the activity of brain depends, and the result is delirium or unconsciousness. There is every reason to believe that the activity of nerve-cells is delicately attuned to surrounding conditions. A small excess per cent. of carbonic acid, or a small amount of what we call a poison, is sufficient to modify or arrest their action. The rhythmic action of various centres, such as those controlling the movements of respiration, is in favour of the view that the activity of such centres depends on delicate equipoises. If during expiration there is for the moment a deficiency of oxygen in the blood, or an accumulation of carbonic acid, the result will be an attempt at inspiration. This gets rid of the carbonic acid and introduces oxygen, and an expiration ensues. It is not pretended here to state what exactly happens, as these phenomena of respiration are still obscure, but they are brought forward with the view of showing that the actions of the rhythmic centres of respiration depend on the delicate balance established between the external conditions and those centres. If this be the case there is little doubt that a similar effect is produced on other centres by the nature of the blood supplied, and that the quality and quantity of the supply are important factors in the production of all conscious conditions.

Nervous centres.

General Phenomena manifested by Nervous Centres.—Before entering on a detailed description of the functions of the great centres such as spinal-cord and brain, it is well to take a survey of some of the general phenomena manifested by such centres. These may be grouped under the heads of (1) reflex actions, (2) inhibitory actions, (3) accelerating actions, (4) vaso-motor actions, (5) secretory actions, (6) sensations, and (7) intellectual acts.

Reflex actions.

Reflex Actions.—Impressions made on sensory nerves are conveyed to nerve-centres, where they may or may not awaken consciousness. A sensation may be defined as the consciousness of an impression, and may or may not be followed by motion. Either motion may be voluntary, or it may be caused by direct stimulation of the motor nerve distributed to the muscles. The latter kind of action in the living body is not common. Usually motor nerves are acted on by the will or by emotional states; but it not unfrequently happens that physical stimuli occasion motion in an indirect manner, the impressions being carried along sensory nerves to a central organ, where changes are excited which result in a discharge of nervous energy along motor nerves to various muscles. Thus a frog in which the brain and medulla oblongata have been destroyed will draw up its limbs if the foot be pinched. Such actions, taking place without consciousness, are called "reflex actions," and the mechanism required for their performance may be thus described: (1) excitation of a sensory or afferent nerve, (2) excitation of an intermediate nervous or reflex centre, and (3) excitation of a motor or efferent nerve, which causes a muscular contraction. The diagram in fig. 6 shows the simplest mechanism; but it is rare to find the arrangements so simple, and the mechanism may become more complex (see fig. 7) either by the existence of a number of cells or groups of cells in the nerve-centre, or by the existence of numerous afferent or efferent nerves. The essence of a reflex action is the trausmutation by means of the irritable protoplasm of a nerve-cell of afferent into efferent impulses (Foster). The following is a brief summary of the leading facts relating to reflex action.

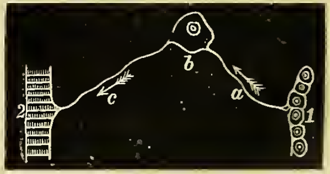

Fig. 6.—Simple reflex action; 1, sensory surface; 2, muscle; *a*. sensory nerve; *b*, nerve-cell; *c*, motor nerve. The arrows indicate the direction in which the influence travels.

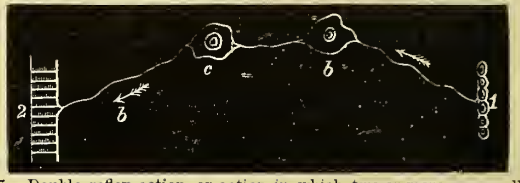

Fig. 7.—Double reflex action, or action in which two or more nerve-cells are involved; 1, 2, as in fig. 6; *a*, motor nerve; *b*, *c*, nerve cells.

(*a*) The initial excitation may occur both in nerves of general sensibility and in those of the special senses; but certain nerves more easily excite reflex actions than others. Thus when light falls on the retina there is contraction of the pupil, the afferent nerve in this case being the optic (see vol. viii. p. 821 *sq.*).

(*b*) A reflex movement may occur whether we excite a sensory nerve at its commencement or at some point in its course, but in the latter case the action is less intense than in the former.

(*c*) Grey matter containing nerve-cells constitutes the chief portion of reflex centres, and groups of such reflex centres are frequently associated by internuncial fibres. The excitability is increased when these centres are severed from communication with psychical centres which preside over voluntary movements. Thus, after decapitation, reflex movements occur with greater intensity than in the injured animal; they are also more active during sleep. It is evident, therefore, that reflex actions may be restrained or hindered in their development by the action of higher centres. This is termed the "inhibition of reflex action."

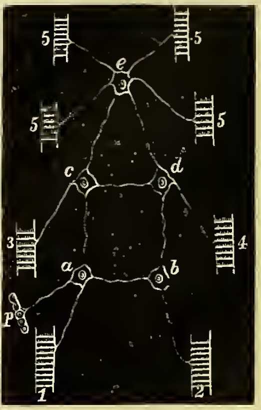

Fig. 8.—*p*, sensory surface; *a*, *b*, *c*, *d*, *e*, nerve-cells; 1, 2, 3, 4, 5, 5, 5, 5, muscles.

(*d*) Reflex movements may occur in one muscle, or in many muscles or groups of muscles. One or more groups of muscles may be involved according to the strength of the stimulus applied to the sensory surface and the degree of excitability of the reflex centre at the time (see fig. 8). The facts are thus summarized by Pflüger. Unilateral action; if in a decapitated frog we excite the skin of the hind foot *p*, the excitation is transmitted from the centre *a* to the muscles 1 of the foot on the same side. Symmetrical action; if the excitation be more intense, it is transmitted to a centre on the opposite side *b*, and contractions may occur in the muscles of the hind limbs on both sides 1, 2. Irradiation; if the excitation be still increased in intensity, it affects higher centres *c*, *d*, and there may be contraction of the fore-limbs 3, 4. General action; if the excitation be still further increased, it may pass to a still higher reflex centre *e*, and the result is general convulsions.

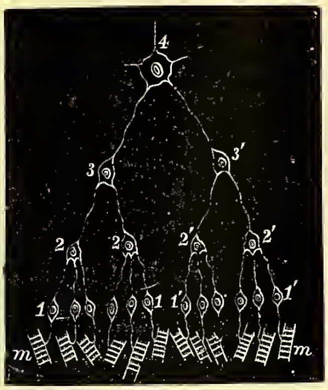

Fig. 9.—Diagram illustrating the superposition of reflexes. *m*, *m*, muscles; 1, 1, series of reflex centres on one side, under the control of 2, 2, which are again governed by 3. There is a corresponding series, 1′, 1′; 2′, 2′; 3′ on the other side. Both sides are presided over by 4. Thus a stimulus reaching 4 might excite the activity of all the muscles *m*, *m*; if it reached 3, only one half of the muscles; if it reached 2, to the left, only three of the muscles; and, finally, if it affected 1, to the left, only one muscle *m*.

(*e*) Reflex centres may be so arranged in the body as to constitute a series in which those of the cerebrum govern or control others in the deeper ganglia of the brain, while these, in turn, have an influence over still lower centres in the spinal cord. This arrangement is termed the "superposition of reflexes" (see fig. 9).

(*f*) Stimulation of a sensory surface may simultaneously produce, by a reflex mechanism, movement, secretion, and consciousness. Thus a condiment in the mouth may cause involuntary twitchings of the muscles, secretion of saliva, and a sensation (see fig. 10).

(*g*) Certain substances, in particular strychnin, increase reflex excitability, so that the slightest external stimulation of the sensory nerves of the skin is sufficient to cause severe convulsions. On the other hand, bromide of potassium, hydrate of chloral, and atropin diminish reflex excitability.

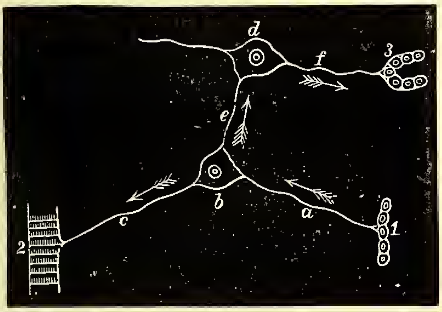

Fig. 10.—Diagram illustrating a complex reflex mechanism. The arrows indicate direction of currents. 1, sensory surface; 2, muscle; 3, gland; *a*, sensory nerve; *b*, reflex centre, connected with another reflex centre *d* by internuncial fibre *e*; *c*, motor or efferent nerve; *f*, secretory nerve passing to gland 3. From the other side of *d* is seen a fibre passing to the brain, and there exciting changes which result in a sensation.

(*h*) Individual stimuli only excite a reflex act when they are very powerful, but stimuli applied at frequent intervals act the more quickly and powerfully the more rapidly they succeed each other. To produce the reflex change in the centre, therefore, a *summation* or addition of centripetal excitations is required. When these reach a certain number the centre responds (Stirling).

(*i*) Reflex actions involve time. Thus the time between the stimulation and the movement can be measured, and, if we take into consideration the time occupied by the passage of the nerve-current along the nerves involved, and the latent period of muscular contraction, and subtract this from the total time, the remainder will represent the time occupied by the changes in the centre or the reflex-time. This has been found to be from ·0555 to ·0471 of a second. It is lengthened by cold and shortened by increasing the strength of the stimulus and by strychnia.

(*k*) In compound reflex acts the initial excitation may occur in psychical centres, as when the recollection of an odour causes nausea, or when a feeling of ennui is followed by a yawn.

(*l*) Some reflex movements are the result of inherited peculiarities of structure, as those made by a new-born child when it seizes the breast. Other reflex movements are acquired during life. Such are at first voluntary, but they become automatic by repetition.

The following are some of the more common examples of reflex movements. Motions of the muscles in any part of the limbs or trunk under the influence of sensory impressions on the skin, such as tickling, pricking, &c.; shuddering from cold, shuddering caused by grating noises, &c.; contraction of the pupil under the influence of light on the retina; winking, from irritation of the sensory nerves of the conjunctiva; sneezing, from irritation of the Schneiderian membrane, or by a glaring light on the eye; spasm of the glottis and coughing, from irritation of the larynx or trachea; laughing, caused by tickling the skin; the first respiration of the child at birth, from the impression of cold upon the nerves of the skin, and especially those of the chest; respiratory movements in the adult, from the impression caused by the afferent nerves of the lungs (sympathetic or vagus), by the presence of carbonic acid in the air cells and passages, or in those of the general system,—also, occasional modifications of the respiratory movements from impressions of cold, &c., on the surface of the body; sucking in infancy; deglutition or swallowing, with all the complicated movements then occurring in the tongue, fauces, larynx, and gullet; vomiting, caused by irritation in stomach, or in fauces, or following nausea; forced contractions of the sphincter muscles of the anus, urinary bladder, and vagina, under local irritation; erection and emission under the influence of irritation of the nerves of the penis and other parts in the vicinity; rhythmic movements of lymphatic hearts in reptiles; rhythmic movements of the heart by the action of cardiac ganglia; peristaltic motions of the stomach and alimentary canal, in digestion and in defecation, &c., under the influence of impressions conveyed to the ganglia by the splanchnic and intestinal nerves; action of the bladder in expelling urine; expulsive action of the uterus in parturition; contractions and dilatations of the blood-vessels under the influence of the vaso-motor system of nerves; many obscure and complex morbid actions, such as palpitations of the heart, cramps in the limbs caused by irritation in the stomach or intestinal canal, fainting from concussion or from peculiar odours, dilatation of the pupil and grinding of the teeth from the irritation of worms, and the convulsive seizure sometimes occurring during teething.

Inhibitory and accelerating actions.

Inhibitory and Accelerating Actions.—As we have seen, stimulation of a nerve may cause a sensation, a reflex action, or the direct contraction of a muscle; but in some instances when the nerve is stimulated movements may be arrested. This occurs where rhythmic and apparently spontaneous or automatic actions are restrained or inhibited by the activity of certain nerves. The most striking instance of inhibition is offered by the heart. The subject will be readily understood with the aid of fig. 11, which illustrates the innervation of the heart and blood-vessels and especially the inhibition and action of the depressor nerve.

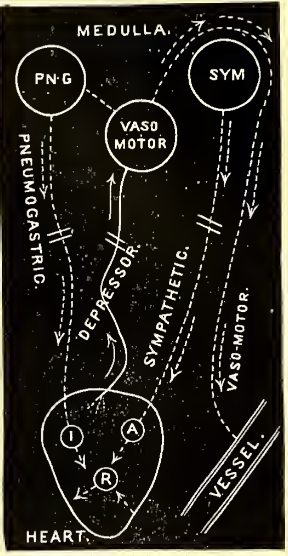

Fig. 11.—The origins of pneumogastric and vaso-motor systems are in medulla, that of the sympathetic in upper portion of cord. The arrows indicate direction of nerve-currents. In the heart R represents a reflex centre, I an inhibitory centre, and A an accelerating centre.

It is well known that the heart of a warm-blooded animal ceases to beat almost immediately after removal from the body, but the heart of a cold-blooded animal, such as the frog, will beat for hours or even days, especially if it be supplied with defibrinated blood. The rhythmic beat depends to some extent on the existence in the heart of ganglia or small nerve-centres (fig. 11, I, A, R). It is quite true, however, that rhythm may go on in a portion of the heart containing no ganglionic structure. Now the heart receives nerves from two sources, from the vagus or pneumogastric nerve and from fibres derived from the spinal cord through the sympathetic. If the vagus be cut and the lower end stimulated by feeble induction-shocks, the heart beats more slowly, and will probably be brought to a stand-still in a dilated condition. A strong stimulation of the vagus will invariably arrest the action of the heart, and the organ will be found dilated, or, as it is said, in a state of diastole. On removal of the stimulus the heart will soon resume its beats. It is clear that the vagus cannot be regarded as the motor nerve of the heart, because, if so, stimulation would have arrested the action of the heart in a state of contraction or systole. The question, then, is whether the fibres of the vagus possessing this remarkable power of inhibiting or restraining the action of the heart terminate in the muscular fibres, or in some intermediate structures, such as ganglia The influence of various poisons has shed light on this question. A minute dose of atropin injected into the blood paralyses this inhibitory action. After such a dose stimulation of the vagus is followed by no effect, and the heart beats as usual.

"Again, in slight urari poisoning the inhibitory action of the vagus is still present; in the profounder stages it disappears, but even then inhibition may be obtained by applying the electrodes to the sinus. In order to explain this result, it has been supposed that what we may call the inhibitory fibres of the vagus terminate in an inhibitory mechanism (probably ganglionic in nature) seated in the heart itself, and that the urari, while in large doses it may paralyse the terminal fibres of the vagus, leaves this inhibitory mechanism intact and capable of being thrown into activity by a stimulus applied directly to the sinus. After atropin has been given inhibition cannot be brought about by stimulation either of the vagus fibres or of the sinus, or indeed of any part of the heart. Hence it is inferred that atropin, unlike urari, paralyses this intrinsic inhibitory mechanism. After the application of muscarin or pilocarpin the heart stops beating, and remains in diastole in perfect stand-still. Its appearance is then exactly that of a heart inhibited by profound and lasting vagus stimulation. This effect is not hindered by urari. The application, however, of a small dose of atropin at once restores the beat. These facts are interpreted as meaning that muscarin (or pilocarpin) stimulates or excites the inhibitory apparatus spoken of above, which atropin paralyses or places *hors de combat*" (Foster, *Text-Book of Physiology*, 4th ed., p. 186).

Thus physiologists are satisfied that, when the vagus is stimulated, currents of nerve-energy pass along its fibres to some of the intrinsic ganglia of the heart and inhibit or restrain these, so that the heart beats more slowly or is arrested altogether. But the centres in the heart may also be stimulated. After division of both vagi in a mammal, say a rabbit, the heart's beat may be quickened or accelerated by stimulation of the cervical spinal cord. Fibres having this power of accelerating the action of the heart have been traced from the cervical spinal cord through the last cervical and first thoracic ganglia of the sympathetic. Stimulation of these *accelerator* nerves causes a quickening of the heart's beat, in which, however, "what is gained in rate is lost in force" (Foster). They are referred to here as showing another kind of nervous action, quite different from inhibition. Thus any nerve-centre concerned in reflex movements may have, by impulses reaching it from the periphery, its action inhibited or restrained or accelerated.

Nerves and blood-vessels.

Influence of Nerves on Blood-Vessels.—If the sympathetic nerve be divided in the neck, there is a dilatation of the vessels and an increase of temperature on the same side; but irritation by weak induction-currents of the cephalic end will cause the vessels to contract and the temperature to fall. In the sympathetic, therefore, there are nerve-fibres which influence the contractile coats of the blood-vessels. These fibres, called "vaso-motor," originate from a vaso-motor centre in the medulla oblongata between the point of the calamus scriptorius and the lower border of the corpora quadrigemina, in the floor of the fourth ventricle. From this chief vaso-motor centre nervous influences emanate which tend to keep the smaller vessels in a more or less contracted condition. If it be injured, paralysed, or destroyed there is at once great dilatation of the vessels, more especially those in the abdominal cavity, and the blood collects in these dilated vessels. This of course diminishes the arterial pressure in the larger vessels. Consequently, by observations on blood-pressure, it has been found possible to study the conditions of vaso-motor action. By connecting a kymograph (a recording manometer) with a large vessel, say the carotid, observing for a time the mean blood-pressure, and afterwards injuring the supposed vaso-motor centre, Ludwig and his pupil Owsjannikoff at once observed an enormous fall of blood-pressure, to be explained by the paralysis of the smaller and a consequent emptying of the larger vessels.

The vaso-motor centre may be influenced—that is, inhibited, or possibly strengthened—by impulses coming from the periphery. Such impulses may be sent to the centre along any sensory nerve, but in 1866 Cyon and Ludwig discovered a nerve which apparently exercises this function to a remarkable extent. In the rabbit it originates by two roots from the superior laryngeal and from the vagus. Stimulation of the distal end of this nerve produces no effect, but stimulation of the cephalic end causes at once a great fall of blood-pressure in the arterial system and a diminution in the frequency of the pulse. As this nerve, therefore, inhibits, restrains, or depresses the activity of the vaso-motor centre it has received the name of the "depressor nerve of Cyon and Ludwig." It appears to influence chiefly the vaso-motor arrangements of the abdomen and lower extremities. Thus, after section of the splanchnics, which control the vessels of the abdominal viscera, it is said that excitation of the depressor does not produce nearly the same diminution of pressure in the carotid vessels. By the influence of the depressor a balance is kept up between the central and the peripheric circulations. Imagine the heart to be pumping blood through the vessels. If from some cause the smaller vessels become constricted so as to offer greater resistance to the passage of the blood, the arterial pressure in the larger vessels is increased, and the heart has more work to do to overcome this resistance. When the resistance reached a certain amount the heart would be in danger of exhaustion in endeavouring to overcome it. But by the depressor this danger is removed, as an influence may pass from the heart along the fibres of the depressor to the vaso-motor centre, the effect of which is to inhibit the activity of this centre, and thus allow the smaller vessels to dilate. When this occurs, either locally, as in the abdominal region, or generally, the result is a depletion of the larger vessels, a consequent fall of pressure in them, and therefore less resistance to the efforts of the heart. Thus it would appear that in the heart itself there is an arrangement by which, to a certain extent, it governs its own work, and there is an adjustment between the activity of the heart and distribution of blood throughout the body (see fig. 11).

The vaso-motor nerves causing contraction of vessels have been called "vaso-constrictors"; but there are other nerve-fibres possessing the property of causing a dilatation instead of a contraction. These have been called "vaso-dilators." Excitation of the chorda-tympani nerve, for example, causes the vessels of the sub-maxillary gland to dilate (see vol. xvii. p. 672). Erection, as it occurs in the penis, has long been known to depend on dilatation of vessels and consequent increased afflux of blood. Stimulation of the nerves of the sacral plexus may cause erection. But how do such nerve-fibres act? It cannot be that they directly cause relaxation of the muscular fibres in the walls of the vessels. These contain layers of involuntary muscular fibres in the transverse and longitudinal directions, and it is difficult to understand how any contraction of fibres in either of these directions could possibly cause dilatation of the vessel. Probably the effect is brought about by the action of some kind of inhibitory mechanism. Ganglia abound in the walls of the vessels. From these, fibres pass to and from the muscular elements of the vessel. Such ganglia or local reflex centres may be supposed to be under the influence of two sets of nerve-fibres: (1) accelerating or strengthening, corresponding to the accelerating fibres that influence the heart; and (2) inhibitory, like the fibres of the vagus distributed to the heart, having the power of restraining the action of the local ganglia. According to this view, the fibres in the chorda which cause dilatation of the vessels of the sub-maxillary gland on stimulation are vaso-inhibitory nerves.

Nerves and glands.

Influence of Nerves on Glands.—This has already been described under NUTRITION (vol. xvii. p. 672), but the facts may be here briefly summarized. A secreting gland is supplied with three sets of nerve-fibres,—vaso-constrictor, vaso-dilator or vaso-inhibitory, and secretory. The first two regulate the distribution of blood in the gland, whilst the third set directly affects the activity of the secreting cells. According to Heidenhain, in addition to the vascular nerves supplying a gland there are secretory and trophic nerves. "Stimulation of secretory fibres leads to an increased flow of water, stimulation of the trophic to an increased secretion of specific substances and to an increased production of protoplasm" (Gamgee). The vaso-constrictor fibres of a gland are derived from the sympathetic, and the vaso-dilator and secretory from the cerebro-spinal system.

Nerve-centres classified.

Classification of Nerve-Centres.—Although these are usually classified anatomically, according to the organ in which they are situated, they may also be arranged according to their functions, as follows:—(1) *receptive* centres, to which influences arrive which may excite sensations (in grey matter of brain), or some kind of activity not associated with consciousness (reflex centres of the cord and of the brain); (2) *psychical* centres, connected with sensation in the sense of conscious perception, emotion, volition, and intellectual acts (in the grey matter of the brain); (3) *discharging* centres, whence emanate influences which, according to structures at the other ends of the nerves connected with them, may cause movements, secretions, or changes in the calibre of vessels (in brain and spinal cord); (4) *inhibitory* centres, which inhibit, restrain, or arrest the actions of other centres.

B.—Special Physiology of Central Organs.

General Physiological Anatomy.—The central organs of the nervous system consist of ganglia or of what is called a "cerebro-spinal axis." The anatomy of the latter is described under ANATOMY, and some account of the gangliated cords in invertebrates and of the rudimentary nervous systems of the lower forms of vertebrates will be found under the articles CRUSTACEA, INSECTS, AMPHIBIA, BIRDS, ICHTHYOLOGY, &c. But, as one of the most effective ways of obtaining an intelligent conception of the complicated nervous system of man and of the higher animals is to trace its various forms in the scale of animal existence, and to observe the close correspondence between complexity of structure and complexity of function, a short introductory review of its comparative anatomy, from the physiological side, will here be given. In the first place, we find that the different forms of nervous systems may be divided into (*a*) those consisting of ganglia or chains of ganglia, as found throughout the invertebrates, and (*b*) those having a great axis of nervous matter forming a brain and spinal cord, the cerebro-spinal axis, as seen in vertebrates.

Nervou system of inve tebrate

Comparative View of Nervous System of Invertebrates.—In the simplest forms of animals the protoplasmic cell is the seat of sensation and of motion; but as the contractile or muscular layers become more marked sensation is relegated to the cells of the ectoderm, or outer layer of the body. As portions of this sensory layer become of higher value to the organism, their protection is accomplished by some of the sensory cells sinking into the body of the organism so as to be covered by less important structures. The portions, originally of the surface, thus differentiated and protected become ganglia, and processes pass from them on the one hand to cells in the periphery, so that they may still be influenced by external energies, and on the other to the contractile parts of the organism by which movements are accomplished. Still higher in the scale of life, the ganglia are connected by internuncial fibres, and the plan of the primitive nervous system bears a relation to the general type of structure of the animal. Thus in radiate animals the gangliated cords show a radiated arrangement, and when the animal form is bilateral and symmetrical the nervous arrangements are on the same type. It is also to be noted that the ganglion specially connected with the rudimentary organs of sense attains a size and importance proportionate to the development of the sense-organs. The nerves of the sense-organs are chiefly connected with the supra-œsophageal ganglion, which thus may be looked on as a rudimentary brain. When the body of the animal becomes more complicated by the development of similar segments (or metameres), we find that by a reduplication, as it were, of the subœsophageal ganglion a ventral chain of ganglia is formed, a pair of ganglia for each segment, the individual ganglia being connected by longitudinal commissures. Such an arrangement is seen in the ringed worms and in arthropods. The next step is a fusion of ganglia into masses, according to the size and importance of the part of the body to be innervated (see vol. vi. p. 636, figs. 7 and 9).

No trace of a nervous system can be detected in *Protozoa*. The Scyphomedusoid forms of *Hydrozoa* show nerve-fibres and ganglion-cells (Schäfer) in the sub-umbrella and around the tentaculo-cysts (see vol. xii. p. 552, fig. 15), and in the Hydromedusoid forms the nerve-ganglion cells form a ring round the margin of the disk. In some of the *Actinozoa* (anemones, &c.) fusiform ganglionic cells united by nerve-fibres are said to exist (P. M. Duncan). In all the worms (*Vermes*) the most important central organs of the nervous system are placed in the anterior part of the body near the beginning of the alimentary canal. If they have a distinct head the nervous organ is in it and supplies branches to the sense-organs. From thence nerve-trunks radiate to the periphery of the body, often in the form of two longitudinal trunks on the ventral surface. Frequently there is a nervous ring round the œsophagus. Nerve-organs have been found in all the *Platyhelminthes*, *Rotatoria*, and *Bryozoa*. The *Nemathelminthes* show a further advance. The central organ is placed on the œsophagus, surrounding it as a ring, from which nerves radiate forwards and backwards. Often six strands of nerve run forwards, whilst a dorsal and a ventral trunk pass backwards. The size of these trunks depends on the length of the body. The cephalic ganglion is bilateral and is largely developed. In the *Hirudinia* and *Annelida* the cerebral ganglia are connected by commissures with a ventral cord, which, in turn, shows individual ganglia connected by commissures. Each ganglion consists of two equal portions with a transverse commissure, and in the higher forms they are so close as to form almost a single cord. It is also evident that the cerebral ganglia are composed of several ganglia fused together, and acquire functional importance as the sense-organs are more highly developed. In the *Echinodermata* the nervous system consists of a number of trunks placed ventrally and having a radial arrangement. Each of these trunks corresponds to the ventral ganglionic chain of the *Annulata*. In *Asterida* (star-fishes) each radial nerve consists of two bands thickened in the middle, and at the end there is a swelling connected with an optical apparatus placed there. In the *Echinus* (sea-urchin) the nervous ring lies above the floor of the oral cavity, between the œsophagus and the lips of the ossicles of the masticatory apparatus. From this ring lateral branches issue which accompany the branches of the ambulacral vessels. In *Holothuroida* (sea-cucumbers) the nervous ring lies in front and near the mouth, and is thicker than the five nerves which it gives off, thus differing from the *Asteroida* and *Echinoida*. The nervous system of the *Arthropoda* resembles that of the *Annelida*. There is a large ganglion above the œsophagus, the cerebral ganglion, united to a ventral ganglion by two commissures so as to form a nervous ring. From the ventral ganglion a series of ganglia united by commissures extends along the ventral surface of the body. The increased size of the cerebrum is the most striking characteristic, and no doubt bears a relation to the higher degree of development of the sense-organs, more especially those of sight. In some *Crustacea* the optic nerves arise from distinct lobes. As pointed out by Gegenbauer, when the optic organs are reduced or lost the cerebrum becomes so small as to be represented by nothing but a commissure. In the individuals having a large portion of the body composed of similar metameres the ganglia are regular in size, appearing in pairs. On the other hand, in the *Thoracostraca* (crabs, &c.) the anterior ganglionic masses are fused into larger masses so as to correspond to the concrescence of the anterior metameres into a cephalo-thorax. In the abdominal portion of the body, where the metameres are small, distinct, and more or less regular, the ganglia are also distinct and in pairs. In the *Protracheata* (*Peripatus*) the nervous system is simpler, and consists of the œsophageal collar with a double ventral cord having no ganglia or swellings on it, although nerve-cells are distributed through it. In the *Myriapoda* there is a well-marked ventral cord, with ganglia corresponding to the metameres. In the *Arachnida* the ventral ganglia are often reduced in number and fused. They are characterized by the close connexion between the cerebral ganglia and the ventral cord, owing to the extreme shortness of the commissures (Gegenbauer). In the *Scorpions* the nervous system is richly segmented, and remarkable for the large size of the ganglion giving off the pedal nerves. The *Spiders* have a single large ganglion in the cephalo-thorax, no doubt consisting of several ganglia. In the *Acarina* (mites) the cerebral ganglion is extremely small, and the other ganglia are fused so as to form one single mass, giving off nerves all round. These minute animals show a remarkable degree of concentration of the nervous system. In *Insecta* (see fig. 12) the ventral cord traverses the whole length of the body, the ganglia being at equal distances, and all united by commissures. This condition is well seen in the larval condition, and is like the permanent state of the *Myriapoda*. When the insect passes into the adult condition changes occur, consisting essentially of the fusion of ganglia and a shortening of the commissures. The cerebral ganglion is composed primitively of three pairs, and in most cases does not unite with the rest of the ventral cord. It shows hemispheres and a complicated structure. The first ganglion of the ventral cord supplies the organs of the mouth; the three succeeding send nerves to the appendages, feet, and wings; the remaining ganglia are small, except the last, which supplies the generative organs. There is great variety among the *Insecta* in the number of ganglia in the ventral cord, but coalescence always indicates a higher type of structure. The nervous system of the *Brachiopoda* is formed of masses of ganglia near the œsophagus. From these nerve-fibres pass to various parts of the body. There is an œsophageal ring, but the superior ganglion is very small, owing to the absence of higher sensory organs. In *Mollusca* (see vol. xvi. p. 635, fig. 1) the nervous system is divided into a superior ganglionic mass, which lies above the commencement of the œsophagus—the supra-œsophageal or cerebral ganglia—and a ventral mass which is connected with the other by commissures, and forms the inferior or pedal ganglia. They are both paired. The cerebral ganglion is connected with the sense-organs. Both the cerebral and the pedal ganglionic masses really consist of ganglia fused together. This is well shown in some of the lower forms, in which the pedal ganglia are divided, and form an arrangement like the ventral cord of the *Annulata*. The remarkable feature in the nervous system of *Mollusca* is the great development of the visceral ganglia and nerves supplying the heart, branchial apparatus, and generative organs (see vol. xvi. p. 643, figs. 17, 18; p. 644, figs. 20, 21, 22; p. 647, figs. 34, 35; p. 648, fig. 36). In the *Lamellibranchia* the cerebral ganglia are very small, owing to the absence of a head and its sense-organs. In some forms they are placed so much to the side as to be united by a long commissure. There are also two pedal ganglia, of a size proportional to the degree of development of the foot. The visceral ganglionic mass is often the largest. It lies behind the posterior adductor muscle, and is united by long commissures to the cerebral ganglion (vol. xvi. p. 693, fig. 144). The nervous system of the *Gastropoda* is remarkable for the large size of the cerebral ganglia. In the *Pteropoda* the cerebral ganglia either retain their lateral position or approach the pedal ganglia, with which the visceral ganglia are also fused. The three ganglionic masses, cerebral, pedal, and visceral, are also represented in the *Cephalopoda*, but they are more approximated by the shortening of the commissures. The ganglionic masses consequently are of great size, and they are more differentiated than any other ganglia in invertebrates. It is possible to distinguish an outer grey layer, formed of ganglionic cells, surrounding a white layer, composed of fibres (vol. xvi. p. 679, figs. 113, 114, 115). Lastly, in *Tunicata* the nervous system is dorsal, instead of ventral, as in other invertebrates. It is developed from the ectoderm, or outermost layer of the embryo, by an infolding so as to form at first a groove and afterwards a tube. In the Ascidian larvæ this nervous tube reaches throughout the length of the tail, and we have thus the remarkable condition of a dorsal-median nerve-cord, analogous to the cerebro-spinal system of vertebrates. Further, embryologists are of opinion that this rudimentary nervous system is the true central organ, although the greater portion of it disappears by the atrophy of the tail in the passage from the larval to the adult state. (Gegenbauer.)

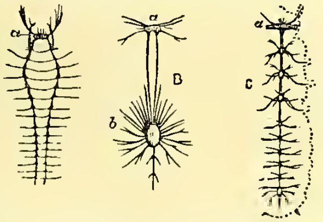

Fig. 12.—Typical forms of nervous system in invertebrates. A, in *Serpula*, a marine annelid; *a*, cephalic ganglion. B, in a crab; *a*, cephalic ganglion; *b*, ganglia fused under cephalo-thorax. C, in a white ant (*Termes*); *a*, cephalic ganglion. (Gegenbauer.)

Nervous system of vertebrates.

Comparative View of Nervous System of Vertebrates.—To understand the structure of the complicated central nervous system of vertebrates, and to appreciate the physiological importance of its various parts, it is necessary to trace its development in the embryo and to note the various forms it presents from the lowest to the highest vertebrates. A consideration of the embryological and morphological aspects of the subject clears up many difficult problems which a study of the human nervous system, by far the most complicated physiological system in the body, fails to do, and in particular it gives an intelligent conception of its architecture, as seen both in simple and complex forms. The cerebro-spinal axis begins in the embryo as a tube of nervous matter produced by an infolding of the epiblast, or outermost embryonic layer. The tube widens at its anterior end, and, by constrictions in its wall, three primary cerebral vesicles are formed, which afterwards become the anterior, middle, and posterior parts of the brain. In the fully-developed condition the cavity of the tube remains as the central canal of the spinal cord and the ventricles of the brain, whilst the various parts of the brain and cord are formed by thickenings in its walls.

Cerebral vesicles.

The three cerebral vesicles have been called the fore-brain, the mid-brain, and the hind-brain. A protrusion from the anterior cerebral vesicle, at first single, but afterwards divided by a median cleft, becomes the rudiment of the cerebral hemispheres (*prosencephala*), the cavity remaining in the adult condition as the lateral ventricle on each side. From each cerebral vesicle another hollow process protrudes which constitutes the olfactory lobe (*rhinencephalon*). What remains of the cavity of the first vesicle becomes the third ventricle (*thalamencephalon*). In the outer and under walls of the *prosencephala* a thickening is formed which becomes the *corpora striata*, two large bodies in the floor of the lateral ventricles of the adult brain, whilst the roof is modified into the substance of the cerebral hemispheres. Immediately behind the corpora striata, and in the floor of the thalamencephalon, two similar thickenings occur which become the *optic thalami*, a thin layer between the two constituting the *tænia semicircularis*, and the Y-shaped canal passing from the cavity between the thalami to the cavities in the cerebral hemispheres (lateral ventricles) is the *foramen of Monro*. The floor of the third ventricle is produced into a conical process, the *infundibulum*, at the blind end of which is the pituitary body, or *hypophysis cerebri*. The roof of this ventricle is very thin, and in connexion with it is developed the pineal gland, or *epiphysis cerebri*. Transverse fibres pass from the one corpus striatum to the others, constituting the *white commissure*, whilst the two optic thalami are connected by two *grey commissures*. In mammals the two cerebral hemispheres are connected by a large and important set of commissural fibres, forming the *corpus callosum*. In addition there are certain sets of longitudinal commissural fibres. Thus two sets of fibres arise from the floor of the third ventricle, arch upwards, and form the *anterior pillars of the fornix*. These are continued over the roof of the third ventricle and run backwards, constituting the *body of the fornix*. Behind this the bands diverge so as to form the *posterior pillars of the fornix*. In the higher vertebrates the upper lip of the foramen of Monro thickens, and becomes converted into a bundle of longitudinal fibres, which is continuous anteriorly with the anterior pillars of the fornix. These are continued back between the inner boundary of the cerebral hemisphere and the margin of the corpora striata and optic thalami, and project into the lateral ventricle, forming the *hippocampus major*. As in highly-formed brains the corpus callosum passes across considerably above the level of the fornix, a portion of the inner wall of the hemisphere on each side and a space between are intercepted. The two inner walls constitute the *septum lucidum*, and the space the cavity of

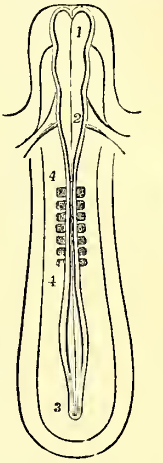

Fig. 13.

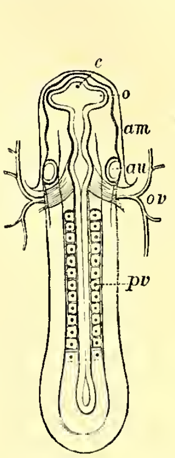

Fig. 14.

Fig. 13.—Outline from above of embryo chick in first half of the second day. 1 to 2, three primary encephalic vesicles enclosed in front and at the sides by the cephalic fold; 3, hinder extremity of medullary canal dilated into a rhomboid space in which is the primitive trace; 4, 4, seven proto-vertebral somites. (Quain's *Anatomy*.)

Fig. 14.—Embryo of dog, more advanced, seen from above (after Bischoff). The medullary canal is now closed in; *c*, anterior encephalic vesicle; *o*, primitive optic vesicle; *au*, primitive auditory vesicle, opposite third encephalic vesicle; *am*, cephalic fold of amnion; *ov*, vitelline veins entering heart posteriorly; *pv*, proto-vertebral somites. (Quain's *Anatomy*.)

the fifth ventricle. By a thickening of the floor of the middle cerebral vesicle (*mesencephalon*) two large bundles of longitudinal fibres, the *crura cerebri*, are formed, whilst its roof is modified into the optic lobes, *corpora bigemina* or *corpora quadrigemina*. The cavity, reduced to a mere tube, is the *iter a tertio ad quartum ventriculum*, or the *aqueduct of Sylvius*. The third cerebral vesicle, *mylencephalon*, undergoes less modification than the others. The upper wall is exceedingly thin before the cerebellum so as to form a lamina, the *valve of Vicussens*, whilst the part behind is covered only by membrane, and opens into the posterior subarachnoid space. The *cerebellum* makes its appearance as a thin medullary lamina, forming an arch behind the corpora quadrigemina across the wide primitive medullary tube. The portion forming cerebellum, *pons Varolii*, and the anterior part of the fourth ventricle is termed the *epencephalon*, whilst the remaining portion, forming the *medulla oblongata* and fourth ventricle, is the *metencephalon*. These facts are briefly summarized as follows (Quain, vol. ii. p. 828).

1. Anterior cerebral vesicle.	*a.* Prosencephalon—Fore-brain.	Cerebral hemispheres, corpora striata, corpus callosum, fornix, lateral ventricles, olfactory bulb (rhinencephalon).
	b. Thalamencephalon — Inter-brain.	Optic thalami, pineal gland, pituitary body, third ventricle, optic nerve (primarily).
2. Middle cerebral vesicle.	*c.* Mesencephalon—Mid-brain.	Corpora quadrigemina, crura cerebri, aqueduct of Sylvius, optic nerve (secondarily).
3. Posterior primary vesicle.	*d.* Epencephalon—Hind-brain.	Cerebellum, pons Varolii, anterior part of the fourth ventricle.
	e. Metencephalon—After-brain.	Medulla oblongata, fourth ventricle, auditory nerve.

The general architecture of the brain considered in this way will be understood by the diagram in fig. 15, whilst details as to the exact anatomy of the human brain will be found under ANATOMY (vol. i. p. 869 *sq.*).

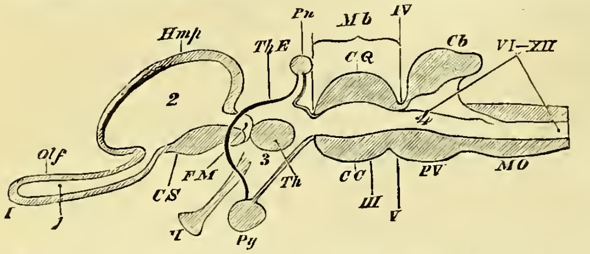

FIG. 15.—Diagrammatic longitudinal and vertical section of a vertebrate brain. The *lamina terminalis* is represented by the strong black line between *FM* and 3. *Mb*, mid-brain, what lies in front of this being the fore-brain, and what lies behind the hind-brain; *Olf*, the olfactory lobes; *Hmp*, the hemispheres; *ThE*, the thalamencephalon; *Pn*, the pineal gland; *Py*, the pituitary body; *FM*, the foramen of Monro; *CS*, the corpus striatum; *Th*, the optic thalamus; *CQ*, the corpora quadrigemina; *CC*, the crura cerebri; *Cb*, the cerebellum; *PV*, the pons Varolii; *MO*, the medulla oblongata; I, olfactorii; II, optici; III, point of exit from the brain of the motores oculorum; IV, of the pathetici; V, of the abducentes; VI-XII, origins of the other cerebral nerves; 1, olfactory ventricle; 2, lateral ventricle; 3, third ventricle; 4, fourth ventricle. (Huxley.)

The complex structure of the brain in the higher animals arises to a large extent from the great development of the cerebral hemispheres. At a very early period these grow forward and project more and more beyond the region of the first primary vesicle, which, as has been noticed, never advances farther forward than the pituitary fossa (*lamina terminalis*); in expanding upwards they take the place previously occupied by the mid-brain, and fill the most prominent part of the head; and by a downward and lateral enlargement they form the temporal lobes. Thus frontal, parietal, and temporal lobes come to be distinguishable, and somewhat later, by a farther increase posteriorly, the hindmost lobes constitute the occipital lobes, and the cerebrum at last covers completely all the lower parts of the brain. The hemispheres, therefore, which are small in the early embryo of all animals, and in adult fishes permanently, attain so large a size in man and in the higher animals as to conceal all the other parts. Whilst this general development is going on the layer of grey matter on the surface of the hemispheres increases to such an extent as to throw the surface into folds or convolutions. The upper surface of the hemispheres is at first smooth (see fig. 16). The first appearance of division into lobes is that of a blunt notch between the frontal and temporal parts below, in what afterwards becomes the Sylvian fissure. In the fourth and fifth months there appear the vertical fissure, separating the parietal and occipital lobes, and the transverse fissure, called the fissure of Rolando, which divides the frontal and parietal lobes superiorly, and which is peculiarly characteristic of the cerebral type of man and of the apes (Allen Thomson). Then the convolutions appear from the formation of secondary grooves or *sulci*, for even at birth they are not fully perfected; and by the deepening of the grooves and the formation of subordinate ones the process goes on during the first years of infancy. For the convolutions see vol. i. p. 873; also PHRENOLOGY, vol. xviii. p. 847.

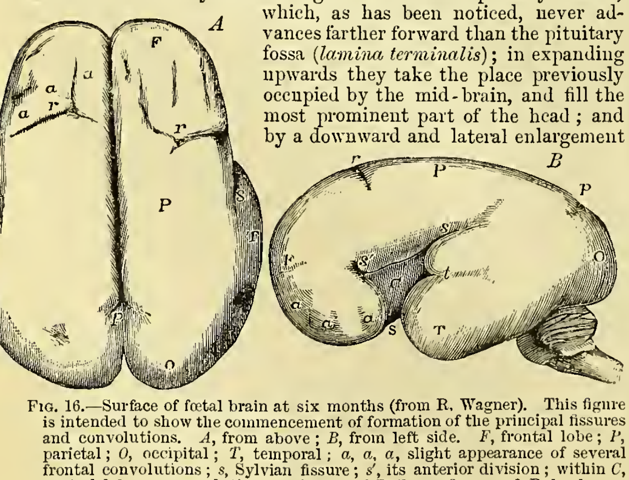

FIG. 16.—Surface of fœtal brain at six months (from R. Wagner). This figure is intended to show the commencement of formation of the principal fissures and convolutions. *A*, from above; *B*, from left side. *F*, frontal lobe; *P*, parietal; *O*, occipital; *T*, temporal; *a*, *a*, *a*, slight appearance of several frontal convolutions; *s*, Sylvian fissure; *s'*, its anterior division; within *C*, central lobe or convolutions of island of Reil; *r*, fissure of Rolando; *p*, parieto-occipital fissure. (Quain.)

Develc ment c brain i animal

The evolution of the brain throughout the animal kingdom shows a graduated series of increasing complication proceeding out of the same fundamental type; so that the forms of brain found permanently in fishes, amphibians, reptiles, birds, and in the lower mammals are repetitions of those shown in the stages of the embryonic series. development of the brain of one of the higher animals.

In the whole class of fishes the brain retains throughout life more or less of the elementary form,—that is, it consists of a series of enlargements, single or in pairs (see fig. 17, C). The simplest of all forms is in the lancelet (*Branchiostoma*), in which there is no distinction between brain and cord, there being no anterior enlargement to form an encephalon. In the *Cyclostomata*, as the lampreys, the form is nearer that of the embryo when the five fundamental parts of the brain can be distinguished. At this stage the cerebrum and cerebellum are extremely small, whilst the ganglia chiefly developed are those connected with the organs of sense, more especially those of vision. In the sharks and skates (*Selachii*, or cartilaginous fishes) the cerebral portion is considerably larger. In osseous fishes (*Teleostei*) the thalamencephalon is so fused with the mesencephalon as to make the homology of the parts difficult to trace, but both cerebellum and cerebrum are still small relatively to the rest of the brain. The most important part of the brain of a fish is the part behind the mesencephalon, as from it all the cerebral nerves originate. Thus not only are the optic lobes relatively important as being the centres of vision, but the medulla oblongata is usually very large. In many sharks it forms the largest part of the brain (Gegenbauer). The spinal lobes of the electric fishes are differentiations of this portion of the encephalon.

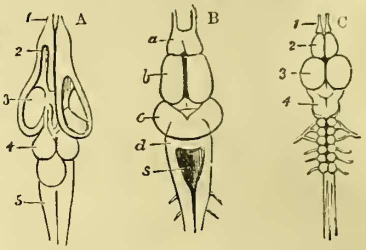

FIG. 17.—Typical forms of brains of lower vertebrates. A. Brain of tortoise (*Testudo*). 1, olfactory; 2, cerebral lobes; 3, corpora striata; 4, optic lobes; 5, medulla. Part of the surface of the cerebral lobes has been removed to show the cavities in the interior, termed "the ventricles." Immediately behind 4, the optic lobes, is the imperfectly-developed cerebellum. B. Brain of common frog (*Rana*). *a*, olfactory; *b*, cerebral lobes covering corpora striata; *c*, corpora quadrigemina, or optic lobes; *d*, cerebellum (rudimentary); *s*, back of medulla, showing fossa. C. Brain of gurnard (*Trigla*). 1, olfactory; 2, cerebral lobes; 3, optic lobes; 4, cerebellum.

In the *Amphibia* the hemispheres are larger, and are divided into two parts (see fig. 17, B). In the *Urodela* (siren, proteus, triton, newt) the mesencephalon remains small, and consists of one lobe, but in the *Anura* (frogs, toads, &c.) there is an advance in this part, it being divided into two. In reptiles there is still an advance in the size of the thalamencephalon and mesencephalon, and the prosencephalon is so large as to pass backwards and overlap the thalamencephalon. The cerebellum (metencephalon) is still small, especially so in *Ophidii* (serpents) and *Saurii* (lizards), but in the *Chelonii* (tortoises, &c.) and in *Crocodilini* (crocodiles, alligators) it is larger. In the crocodile there is a transverse grooving of the cerebellum, giving rise to foliation or laminar division, which is carried much farther in birds and mammals, indicating a greater power of co-ordination or regulation of movement.

In birds (fig. 18) the vesicles of the mid-brain are partially hidden by development of the cerebral hemispheres. These are connected by a fine anterior commissure, and they contain a large amount of ganglionic matter bulging into the primitive cavity or ventricles, which are of very small size. The middle portion of the cerebellum shows a distinctly laminated structure and a differentiation into white and grey matter. But there is no pons Varolii, nor corpus callosum, nor fornix, nor hippocampus. In the floor of the lateral ventricles may be seen a ganglionic mass corresponding to corpus striatum and optic thalamus. The optic lobes are relatively large and show considerable differentiation of structure.

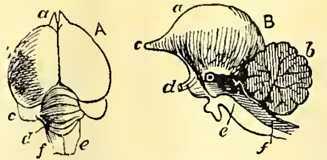

FIG. 18.—Typical brain of bird. A, view from above; B, lateral view of a bisected brain. A.—*a*, olfactory; *b*, cerebral lobes; *c*, optic or bigeminal lobes; *d*, cerebellum; *e*, medulla oblongata; and *f*, spinal cord. B.—*a*, cerebrum; *b*, cerebellum; *c*, olfactory; *d*, optic nerves; *e*, medulla; *f*, spinal cord.

Mammals, even the lower orders, not only show a general enlargement of the cerebral hemispheres, but we find a commissure, the corpus callosum, uniting them. This commissure is of small size, and is confined to the fore part of the hemispheres in *Monotremata* (*Ornithorhynchus*, *Echidna*) and *Marsupialia* (kangaroos, &c.), and in some of the *Edentata* (ant-eaters, sloths, &c.), but it gradually extends farther and farther back as we ascend to the higher orders. The chief changes thus occur in the prosencephalon. In the lower orders of mammals the hemispheres are comparatively small and simple, and do not present any division into convolutions, and very little distinction even of lobes. The cerebral hemispheres gradually grow backwards, covering mid-brain, cerebellum, and medulla oblongata, as we find in the higher *Primates* (monkeys, apes, and man). There is also a general enlargement of the brain and of the cranial cavity. The development of a posterior lobe only takes place in the higher orders, and in these also the enlargement of the frontal lobes brings the front of the cerebrum more and more over the nasal cavities, causing a development of forehead. This also explains how the olfactory bulbs in more highly-formed brains are thrown below the frontal part of the hemispheres, instead of originating at their anterior borders. But the internal arrangements of the brain also become more complicated. The fornix, already described, establishes, by its longitudinal commissural fibres, a connexion between the anterior and posterior lobes of the cerebrum. In the *Monotremata* and *Marsupialia* the mid-brain retains a bifid form, constituting the optic lobes, or corpora bigemina, but in all higher animals each is divided into two by a transverse groove, forming the corpora quadrigemina, of which the anterior pair is the largest. As we ascend also, we find the surface of the brain becoming more and more convoluted (see figs. 19 and 20). This is the general fact; but whilst the convolutions are most numerous and deepest in the highest orders there is no regular gradation, as in each group there are very great variations in the degree of convolution (Allen Thomson). Thus in the *Monotremata* the *Echidna* has a more convoluted cerebrum than the *Ornithorhynchus*, whilst in the *Primates* the brains of the marmosets show a comparatively smooth non-convoluted surface, in striking contrast to the rich convolutions seen on the brains of the higher monkeys and of the apes. It is important to note that the cerebellum also becomes more and more complicated as we ascend from the lower to the higher groups. At first merely a lamina or band, as seen in fishes and amphibia, it is a centrally differentiated body in crocodiles. In birds there is an indication of a division into three portions, a central and two lateral, whilst the central is by far the larger, the two lateral being feebly developed. In *Monotremata* the central portion is larger than the lateral, but, whilst it is larger in *Marsupialia*, *Edentata*, and *Cheiroptera* (bats, &c.), it is clear that the lateral portions are increasing in size so as to make the disproportion less. But in *Carnivora* (felines, hyæna, otter, bear, &c.) and in *Ungulata* (sheep, ox, camel, rhinoceros, horse) the lateral lobes, or hemispheres, of the cerebellum develop to a much greater size; and in most of the *Primates* they are much larger than the median portion, which is now called the worm or "vermiform process." As regards the development of the spinal cord continuous with the medulla oblongata, it need only be said that it does not show any marked peculiarities of structure in different animals. The grey matter from which nerve-fibres originate and in which they end is found in the centre of the cord, and it is most abundant in the regions associated with the development of limbs. The white matter is external, and, in the cords of the higher animals, can be differentiated by fissures into columns, the special functions of which will be hereafter considered. The size of the cord is influenced by the masses of nerves given off from it, so that it attains its greatest thickness and development in the four higher divisions of the vertebrates possessing limbs. Thus, too, are formed cervical, dorsal, and lumbar enlargements, contrasting with the more uniform and ribbon-like form of the cord in fishes, although even in these there are special enlargements corresponding to the points of exit of important spinal nerves.

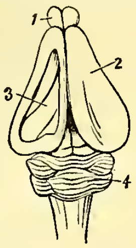

Fig. 19.

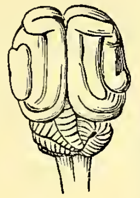

Fig. 20.

FIG. 19.—Rabbit's brain. 1, olfactory; 2, surface of cerebral hemisphere; 3, lateral ventricle, on the floor of which is seen the corpus striatum; 4, cerebellum.

FIG. 20.—Cat's brain, showing convoluted surface. Contrast the form of the cerebellum in the cat and the rabbit. In the cat the central lobe is small, whilst the lateral lobes are largely developed.

Size and weight of brain.

Size and Weight of Brain.—The gradual increase in the size of the brain, as compared with that of the body, which is observed as we rise in the animal scale, has some intimate proportional relation to a corresponding increase of the nervous and mental endowments. Information as to the size of the brain may be obtained by direct measurement of dimensions and weight; but as this is often difficult recourse may be had to the measurement of the capacity of the cranium, which contains, however, not only the brain but its accessories, such as membranes and blood-vessels. Details will be found in vol. i. p. 879. After considering the measurements of several thousand skulls made by different observers, the late Dr Allen Thomson arrived at the conclusion that the cranial capacity is on the whole greater among the highly-civilized than among the savage races, and that there is even a very manifest difference to be found between persons of higher mental cultivation and acknowledged ability and those of the uneducated class and of inferior intellectual powers; and he states further that the amount of this difference may be from 5 to 7½ per cent. in persons of the same race, and about double that range in those of different races. Thus, the average adult brain of men in Britain being taken at 3 ℔, or, more precisely, at 49½ oz. avoir. (women, about 44 to 44½ oz.), at an average specific gravity of 1040, would give a bulk of 82·5 cubic inches of brain-substance; 10 per cent. being deducted for loss by membranes, fluid, &c., the cranial capacity will be about 90 inches. Conversely, the weight of the brain may be calculated from the known cranial capacity. If, therefore, the brain of the uneducated class falls 2·5 oz. below the average, whilst that of the more cultivated persons rises to the same amount above it, or to 52½ oz., we may regard these brain-sizes as corresponding with brain-bulks and cranial capacities of 78 and 87 cubic inches, and of 88 and 97 cubic inches respectively. The average brain-weight of an Australian aboriginal man is about 42 oz., corresponding to a brain-bulk of about 70 cubic inches, and a cranial capacity of about 78 cubic inches. There are, however, great variations in all races. Thus the brain of Cuvier, the great naturalist, weighed 65 oz. avoir., corresponding to a brain-bulk of 108 cubic inches and a cranial capacity of 118 cubic inches; whilst, on the other hand, in Europeans the brain-weight has fallen as low as 32 oz., or a brain-bulk of 53 cubic inches and a cranial capacity of 63 cubic inches. The brains of the anthropoid apes—gorilla, chimpanzee, and orang—are all inferior to man in their dimensions. In the gorilla the brain does not attain more than a third of the weight of the average human brain, and in the chimpanzee and orang it does not reach a fourth, so that the ratio of brain-weight to body-weight in these animals may be as 1 to 100, whilst in man it ranges from 1 to 40 to 1 to 50. It is remarkable that in general among the largest animals of any group the brain does not reach a size proportionate to the greater magnitude of the other organs or of the whole body, so that in the smaller members of the same order a considerably greater proportional size of the brain is observed. Thus in the small marmosets the proportion of the brain-weight to the body-weight may be 1 to 20, or more than double the proportion in man. Similar facts are brought out in comparing the brains of cetaceans, pachyderms, dogs, &c., as shown in the following table.

Table of comparative sizes of Brain and Body.

Examples.	Brain-weight in oz. avoir.	Internal cranial bulk in cub. in.	Whole weight of the body in ℔.	Proportion of brain to body weight
Average European man	48 (3 ℔)	85 to 88	140	1 to 46
Child at birth	12	22	7½	1 to 10
Chimpanzee	10	19	50	1 to 80
Marmoset	⅓	½	6 oz.	1 to 18
Middle-sized dog	3½	6	36	1 to 164
Small dog	2½	4½	7	1 to 45
Elephant..............	144 (9 ℔)	300	6,720 (3 tons)	1 to 747
Pig	6	11	94	1 to 250
Whale[1]	96 (6 ℔)	650	134,400 (60 tons)	1 to 22,400
Porpoise	16	30	60	1 to 60

Although the proportion of brain-weight to body-weight in a male child at birth is 1 to 10, yet so rapidly does the brain continue to grow during the early period of childhood that by the age of three years it has attained more than three-fourths of its full size, by the age of seven years it has reached the proportion of nine-tenths, and after this, only by slow and small gradations, it attains the full size between the ages of twenty and twenty-five years.[2] See PHRENOLOGY.

Comparative development of brain.

From this survey of the comparative development of the brain the following general conclusions can be drawn.

1. The first and essential portion of the cerebro-spinal axis is the portion forming the spinal cord and medulla oblongata, inasmuch as it is found throughout the whole range of vertebrate existence, and is connected with the reflex or automatic movements on which locomotion, respiration, and the circulation more or less depend, and with the simple sense of contact, or touch, or pressure. This portion is necessary to mere existence.

2. When higher senses are added, such as those of taste, smell, hearing, vision, portions of the anterior part of the cerebro-spinal axis are differentiated so as to form centres. The earliest and most important of these senses (next to touch) is vision, hence the high degree of development of the optic lobes even in the lowest forms; to these are added the optic thalami, which may be regarded as the centres of tactile sensations involving appreciation of differences of touch as to softness, smoothness, hardness, &c., requiring in the periphery special terminal organs. Special centres for hearing, taste, and smell are not differentiated. It is remarkable that the organs relating to the sense of smell are most anterior and most closely related with the prosencephalon, indicating, apparently, that this sense is one of the earliest in appearance, and probably, along with vision and touch, one of the most necessary to existence.

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[1] The large cranial bulk in this instance is connected with the enormous size of the roots of the cranial nerves.

[2] Many of the facts of this paragraph as to size and weight of brain are derived from an unpublished lecture by the late Dr Allen Thomson.

It is equally striking that the origin of the auditory nerves should be placed so far back as in the medulla oblongata and cerebellum, indicating the primitive nature of simple auditory impressions and their relation to co-ordination of movement. The sense of taste originates in nerves springing from the medulla, and in close connexion with those regulating the movements of the tongue and swallowing.

3. When sensations of a simple character are elaborated into ideas and give rise to the physical changes in some way correlated to mental states, involving memory, emotions, volitions, and intellectual acts, a part of the cerebro-spinal axis is differentiated for these functions in proportion to the extent to which such mental phenomena are manifested by the animal. Judging from the facts obtained by comparing animal intelligences, so far as they can be appreciated by us, we have the right to infer that in proportion to the degree of development in size and complexity of structure so is the mental condition of the animal. Taking it broadly, there can be no question that the intelligence of a bird is higher than that of a reptile, amphibian, or fish, and that the intelligence of the higher mammals, such as one of the *Primates*, is superior to that of the lower, as one of the *Insectivora* (hedgehog), or of the *Marsupialia* (kangaroo); and along with the higher intelligence is the more complex brain. There are qualifications to this statement to be afterwards alluded to, but they arise from deficient knowledge and do not vitiate the main conclusion. In proportion, therefore, to the degree of development of the prosencephalon do we find the intelligence of the animal, and we may regard this portion as superadded to the cerebro-spinal axis as the organic mechanism for such mental operations.

4. There is also a correspondence between the degree of development of the cerebellum and the faculty of co-ordination of movement. Movements of the members of the body may be of a very simple character, or they may be very complex. They may be due to the action only of flexor and extensor muscles, causing the limb to move almost in the same plane, or they may be associated with the action of adductor and abductor muscles, by which there may be many kinds of circular or rotatory movements. There is a great difference between the movements of a fish's fin, of a bird's wing, of a horse's fore-leg, and of the arm of a monkey or a man. In the first three they are almost to-and-fro movements, unlike the delicate movements of flexion, extension, pronation, supination, and prehension seen in the latter. Delicacy of movement of the anterior limb reaches its highest condition in man. It may be put generally that simplicity of movement is associated with an imperfectly-developed cerebellum, whilst in animals having the power of complicated movements, involving especially the knowledge of how the limbs are acting at any moment, and of adjustment of movement in special circumstances, the cerebellum is highly developed. From this point of view, the degree of development of the cerebellum is as characteristic of man as the degree of development of the cerebrum. That this is no accidental correspondence will be shown in treating of the functions of the cerebellum.

Having reviewed the physiological anatomy of the cerebro-spinal system, an account will now be given of the more special physiology of the centres composing it,—namely, spinal cord, medulla oblongata, pons Varolii, basal ganglia (including corpora striata optic thalami, and corpora quadrigemina), cerebellum, and hemispheres of the cerebrum.

Spinal cord.

Spinal Cord.—The spinal cord is described at vol. i. p. 865 *sq.*, but it is necessary here to allude to a few points of physiological importance. The cord consists externally of white and internally of grey matter. The white matter, composed of nerve-fibres, forms a series of strands or columns in each half of the cord. The grey matter in the central part of the cord is arranged in two crescentic masses, and shows under the microscope numerous multipolar cells connected with nerve-fibres and imbedded in neuroglia, or the special connective tissue of the nerve-centres. The neuroglia is composed of a kind of semi-fluid matrix, fibrils, and peculiar cells having numerous branches called "Deiter's cells." (See fig. 21.) These nerve-cells are arranged in definite groups and occupy the same relative position in successive sections, forming the ganglionic or vesicular columns of the grey matter, as follows. (1) Cells found along the whole of the anterior part of the anterior cornua, many of the processes of the nerve-cells being continuous with the nerve-fibres of the anterior roots of the spinal nerves. This column of nerve-cells has been called the "motor ganglionic column," or the "vesicular column of the anterior cornua." (2) A group or column of nerve-cells at the inner or mesial angle of the base of the posterior cornu, in the middle region of the cord from the third lumbar to the seventh cervical nerve. This is termed the "posterior vesicular column," or "Clarke's column," after the late Mr Lockhart Clarke, who did much to unravel the intricate anatomy of the nerve-centres. The nerve-cell processes are continuous chiefly with nerve-fibres coming from the lateral column. This vesicular column is best developed where the column of the anterior cornu is least so. (3) The third column of nerve-cells is in the outermost portion of the grey matter, midway between the anterior and posterior cornua. Development has shown that at an early period the anterior horns are distinctly differentiated from the posterior, and that the grey matter between them is the last to be formed. The nuclei in the latter may be regarded, therefore, as accessory nuclei. It has also been observed by Flechsig and others that the white substance of the cord also makes its appearance first in the neighbourhood of the anterior and posterior roots. The cord at a very early period consists almost entirely of grey matter, and the columns are superadded in the anterior first, the posterior last. The posterior can also be traced to the cortex of the cerebellum (Flechsig).

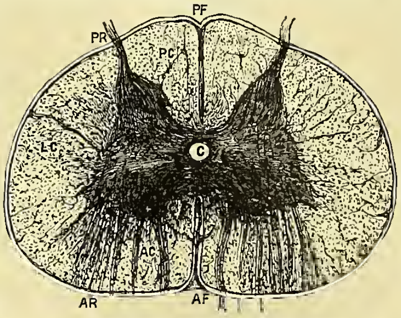

Fig. 21.—Transverse section through spinal cord. *AF*, antero-median, and *PF*, postero-median fissures; *PC*, posterior, *LC*, lateral, and *AC*, anterior columns; *AR*, anterior, and *PR*, posterior nerve-roots; *C*, central canal of cord, with its columnar epithelial lining. The crescentic arrangement of the grey matter is shown by the darker-shaded portion.

The anterior and posterior roots of the spinal nerves are attached along the sides of the cord, opposite to the corresponding cornua of grey matter. Some of the fibres of the anterior roots end in nerve-cells in the anterior cornu. Others pass through the grey matter and cross to the other side of the cord through the anterior commissure, a layer of white matter at the bottom of the anterior median fissure. A third set passes to the anterior part of the lateral column and to the posterior cornu. The course of these fibres is shown in fig. 22. A portion of the fibres of the posterior roots ends in the grey matter on the same side, but many cross to the grey matter on the opposite side. There is thus a decussation of fibres connected with both the anterior and the posterior roots. The arrangement of the white or fibrous columns of the cord is seen in the table under medulla oblongata below.

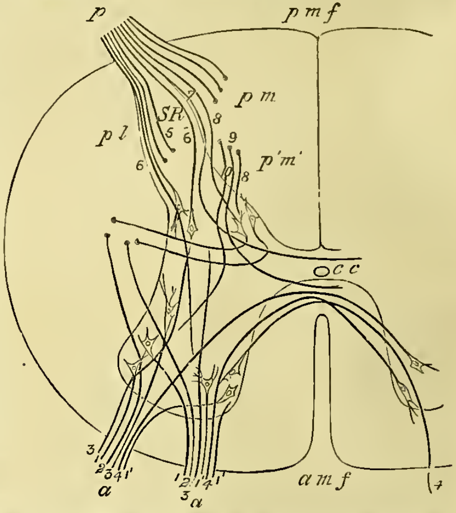

Fig. 22.—Diagram to illustrate the course taken by the fibres of the nerve-roots on entering the spinal cord (Schäfer; Quain's *Anatomy*). *a*, *a*, two funiculi of anterior root of a nerve; 1, 1, some of their fibres passing into lateral cells of anterior cornu; 1′, 1′, others passing into mesial cells of same cornu; 2, 2, fibres passing to lateral column of same side without joining nerve-cells; 3, 3, fibres passing towards posterior cornu; 4, 4, fibres passing across anterior commissure, to enter nerve-cells in anterior cornu of other side; *p*, funiculus of posterior root; *pl*, fibres of its external or lateral division coming through and around gelatinous substance of Rolando; some of these (5) are represented as becoming longitudinal in the latter, others (6, 6) as passing towards anterior cornu, either directly or after joining cells in posterior cornu, and others (7) as curving inwards towards grey commissure; *pm*, fibres of mesial or inner division, entering into posterior column and then becoming longitudinal; *p′m′*, fibres from a posterior root which had joined the cord lower down and entered posterior column, now passing into the grey matter at root of posterior cornu. Of these, 8 is represented as entering Clarke's column, 9 as curving round this and coursing to anterior commissure, and 10 as passing towards anterior cornu,—the axis-cylinder processes of the cells of Clarke's column are shown arching round and taking the direction of the lateral column; *amf*, anterior median fissure; *pmf*, posterior median fissure; *cc*, central canal; *SR*, substantia gelatinosa of Rolando.

The spinal cord acts (1) as a transmitter of motor and sensory—or centrifugal and centripetal—impressions between the encephalon and the periphery, and (2) as a reflex centre.

Motor and sensory impressions.

1. *Transmission of Motor and Sensory Impressions.*—Each spinal nerve, as already mentioned, is connected with the spinal cord by and two roots, an anterior and a posterior. Section of a number of anterior roots causes paralysis of motion of muscles on the same side of the body, whilst irritation of the distal or peripheral end of the divided roots causes twitchings or tetanus of the muscles. Neither section nor irritation has any effect on sensation. Hence the anterior roots contain motor fibres, carrying impressions from

the cord outwards. Again, section of a number of posterior roots is followed by loss of sensation of a part of the body on the same side, and, if the proximal ends of the divided roots—those next the cord—be irritated, painful sensations are excited. The posterior roots, therefore, contain sensory fibres, carrying impressions into the cord from the periphery. As we have seen, these roots are connected with the grey and white matter of the cord, and it is practically impossible to trace all their ramifications. Recourse must therefore be had to the evidence supplied by experiment (cutting, or by the Wallerian method, p. 26) and by pathological observation. In tracing the path of fibres, what may be called the "developmental method" has been pursued. It has been shown by Flechsig that, "if the development of the cord be carefully observed, the medullary substance of the nerve-fibres is formed later along certain tracts of the white columns than in the rest of the white matter, so that in transverse sections of the cord these tracts are easily distinguishable by their more transparent grey appearance" (Quain, vol. ii. p. 277). If the anterior columns be cut by an incision extending into the grey matter, leaving the posterior columns intact, voluntary movements disappear in the parts below the section. Again, section of the posterior columns and grey matter, leaving the anterior uninjured, enfeebles but does not destroy the power of voluntary movement below the section. Finally, section of an antero-lateral column on one side paralyses voluntary motion on the same side. From these facts it is inferred (*a*) that the motor tracts passing from the brain to the periphery are in the antero-lateral columns, and (*b*) that the fibres forming these tracts are chiefly distributed to the same side of the body. These inferences are supported by pathological observation. In diseases where the anterior horns of grey matter are affected paralysis ensues, with complete flaccidity of the limbs; and if, from hæmorrhage, softening, or the pressure of tumours, the anterior portion of the cord be irritated there are spasmodic twitchings of muscles. Complete transverse section of the posterior columns does not abolish sensibility in the parts below; but there is a loss of the power of making co-ordinated movements. Section of the posterior columns and of the antero-lateral columns, leaving only the grey matter in the centre of the cord intact, does not abolish sensibility. Again, section of the antero-lateral columns and of the whole of the grey matter, leaving only the posterior columns uninjured, is followed by complete loss of sensibility in the parts beneath. The inference therefore is that sensory impressions pass through the grey matter. As already seen, many of the sensory fibres connected with the posterior roots decussate in the grey matter. This explains some of the results obtained by Brown-Séquard, that hemi-section of the cord, involving the grey matter, enfeebled sensibility *on the opposite side* more and more as the section cut deeply into the grey matter; that a vertical section in the bottom of the posterior median fissure caused loss of sensibility on both sides; and that a lateral section, whilst it caused loss of sensibility (anæsthesia) on the opposite side, was followed by increase of sensibility (hyperæsthesia) on the same side,—a curious fact, explained by Brown-Séquard as being due to irritation caused by paralysis of the vessels of the cord on the side of the section. It would appear also that tactile impressions travel, for a certain distance at all events, in the posterior columns. This has been inferred chiefly from the fact that in certain cases of paralysis involving the posterior columns, where the sensation of touch was absent, the patient could still feel a painful sensation, as when a needle was thrust into the skin; whilst in other cases, in which these columns were not affected, the converse held good. In the disease known as locomotor ataxia (see ATAXY and PATHOLOGY, vol. xviii. p. 392) the patient first passes through a period in which there are disorders of general sensibility, especially lancinating pains in the limbs and back. By and by there is unsteadiness of gait when the eyes are closed or in the dark, and to a large extent the patient loses the power of co-ordinating movement. Especially he is unable to judge of the position of the limbs without seeing them; in other words, the so-called muscular sense is enfeebled. At last there is a stage before death in which there is almost complete paralysis. A study of this disease has thrown much light on the physiology of the cord. It is known to be caused by a slow disorganization or sclerosis of the posterior root-zones, the posterior columns,—slowly passing on to affect the columns of Goll, the lateral columns, and the anterior grey horns, and ultimately involving the cord. The disordered sensations at an early stage, the staggering gait at a later, show that the posterior part of the cord has to do with the transmission of sensory impressions. The man staggers, not because he is paralysed as regards the power of movement, but because, in consequence of the sensory tracts being involved, he does not receive those peripheral impressions which excite or indirectly regulate all well-ordered movements of locomotion.

2. *As a Reflex Centre.*—The grey matter of the lower cervical, dorsal, and lumbar regions of the cord may be regarded as composed of reflex centres associated with the general movements of the body, whilst in the upper cervical region there are more differentiated centres corresponding to special actions. The initial excitation may commence in any sensory nerve; the effect passes to the cord, and sets up changes in the nerve-cells of the grey matter, involving time, and resulting in the transmission outwards along motor fibres of impulses which excite particular groups of muscles. There is an exact co-ordination, with a given strength of stimulus, between certain areas of skin and certain groups of muscles, and thus movements may be so purpose-like as to simulate those of a conscious or voluntary character. Thus irritation near the anus of a decapitated frog will invariably cause movements of the limbs towards the irritated point. The activity of reflex centres may be inhibited, as already shown, by higher centres, or possibly by certain kinds of sensory impressions reaching them directly from the periphery. Hence removal of these higher centres is followed by apparently increased reflex excitability. Strychnia and the alkaloids of opium increase it, whilst aconite, hydrocyanic acid, ether, chloral, and chloroform have an opposite effect. In certain pathological conditions also, as in tetanus, or in some slow progressive diseases of the cord, reflex excitability may be much increased. In tetanus the slightest touch, a movement of the bedclothes, the closing of a door, the vibration caused by a footstep, may throw the patient into severe and prolonged convulsions. The earlier formed ganglionic cells are those specially concerned in reflex acts.

Special reflex centres.

Special reflex centres have been clearly made out in the cord. (1) A *cilio-spinal* centre, between the sixth cervical and third dorsal nerves, associated with the movements of the iris. The fibres controlling the radiating fibres of the iris, and found in the sympathetic, originate here (see EYE). Hence irritation of this region causes dilatation of the pupil, an effect not produced if the sympathetic fibres have been divided. (2) *Accelerating* centres, supplying fibres to the sympathetic which ultimately reach the heart, and irritation of these centres quickens the movements of that organ. (3) *Respiratory* centres. The movements of respiration, of a reflex character, involve the action of many thoracic and abdominal muscles. Section of the cord above the eighth dorsal paralyses the abdominal muscles; above the first dorsal, the intercostals; above the fifth cervical, the serratus magnus and the pectorals; and above the fourth cervical, by paralysing the phrenics, it arrests the action of the diaphragm. (4) *Genito-spinal* centre. This is in the lumbar region. Irritation causes erection, &c.; destruction or disease is followed by loss of virile power. (5) *Ano-spinal* and *vesiculo-spinal* centres. These, connected with the movements of the sphincter ani and of the bladder, exist in the lower portion of the dorsal and upper portion of the lumbar regions. Disease or injury involving these centres causes involuntary evacuation of the bowel and complete paralysis of the bladder, with non-retention of urine. The bladder may be full whilst the urine constantly escapes in small quantity.

Cord as trophic centre.

3. *As a Trophic Centre.*—The ganglion-cells in the anterior cornua undoubtedly have a trophic or nutritive influence upon muscles. This has been determined chiefly on pathological evidence. If these cells undergo atrophy or degenerative changes, the muscles, even though they may be kept periodically in a state of activity by galvanism, become soft and fatty changes take place. There is thus a correlation between the nutritive condition of muscle and nerve-centre, and influences affecting the one affect the other also.

It has been supposed that the cells in Clarke's vesicular column may form the centres in visceral innervation. They are bipolar, like those in the sympathetic, and not multipolar as in the rest of the cord, and the columns are absent in the lumbar and cervical enlargements. The cells are found where nerves come off that influence the viscera, and similar cells are found at the roots of the vagus in the medulla,—a nerve also much concerned in the innervation of viscera.

Inhibition of reflex actions.

Inhibition of Reflex Actions.—The reflex actions of the spinal cord may be *inhibited* or restrained to a greater or less extent by the action of centres in the encephalon, so that pure reflex actions only occur after removal of the cerebrum, or during profound sleep, when the cerebrum is inactive. Thus a strong effort of the will may restrain from scratching an irritated part of the skin, whilst the same amount of irritation would certainly cause reflex movements if the will were in abeyance. Such power of voluntary control, however, is limited with respect to most reflex actions, whilst some reflex acts cannot be so influenced. Any movement that may be orginated by the will may be inhibited or restrained to a certain extent when the movement is of a reflex character; but, if the movement be invariably involuntary, it can never be inhibited. Thus the ejaculation of semen cannot be voluntarily induced, whilst the reflex act once provoked cannot be arrested (Hermann). That these inhibitions of reflex actions of the cord depend on mechanisms in the brain is proved by the fact that removal of the brain is followed by an increase in the reflex excitability of the cord, and that even section of the cord permits of increased reflex excitability below the plane of section (Setschenoff). Further, after section of the spinal cord in the cervical region, irritation of the lower end arrests reflex movements dependent on reflex centres in the lower cervical, dorsal, and lumbar regions (M'Kendrick).

Medulla oblongata.

Medulla Oblongata.—This is the prolongation into the cranium of the spinal cord so as to unite it with the brain. Strictly speaking, the medulla spinalis and the medulla oblongata form one organ. The columns of white matter of the cord undergo changes in form, structure, and relative position when they pass into the medulla (see vol. i. p. 870). Without again detailing the minute anatomy, it is necessary to show, as in the following table, the connexions of the cord and of the medulla with the rest of the brain.

	Columns of the Spinal Cord.	Divided into	Continued in Medulla Oblongata as	Pass on to
Antero-lateral column.	A. Pyramidal tract.	*a*. Lateral, or crossed, fibres from the posterior part of the lateral column as low as the third or fourth sacral nerves.	Decussate in anterior pyramids.	Cerebrum.
		b. Anterior, or uncrossed, fibres from the dorsal region of the cord-columns of Türck, or columns of Lockhart Clarke.	Pass under pyramid on same side, and form longitudinal fibres of the reticularis alba in dorsal part of mesial area. 1. Posterior longitudinal bundle in pons. 2. Tract of the fillet.	Cerebrum. Corpora quadrigemina.
	B. Cerebellar tract.	*c*. Cerebellar tract, between lateral pyramidal tract and the outer surface of the cord as low as the second or third lumbar.	Restiform body.	Cerebellum.
	All the antero-lateral columns except A and B.	*d*. Principal tract of anterior column, that is, the antero-lateral column less the fibres in *b*. Not continued up—probably commissural from one side of cord to the other.	....	....
		e. From anterior column.	Pass below olivary body to form part of restiform body. Sometimes called the "band of Solly"—not always present.	Cerebellum.
	Posterior column.	*a*. Posterior white column, or Goll's tract, from middle of dorsal region.	....	....
		b. Posterior lateral column, between posterior median column and postero-lateral groove.	Posterior median column, becoming the funiculus gracilis, which, with the expansion called the clava, becomes the posterior pyramids.	Cerebrum.
		c. Funiculus of Rolando, between the posterior lateral column *b* and postero-lateral groove higher up.	Funiculus cuneatus, forming, with cerebellar tract from antero-lateral column, the restiform body.	Cerebellum.

It is important to note the fact that each column of the cord, through the medulla, is thus connected both with the cerebrum and with the cerebellum. Development has shown that the fibres of the bundles which are first formed develop a medullary sheath at a time when the fibres of the later-formed bundles are non-medullated. "When the cord of a human embryo is examined at the end of the fifth month it will be found that the pyramidal fibres of the lateral columns, the fibres of the columns of Türck, and of the columns of Goll are non-medullated; while the fibres of the anterior and posterior root-zones and the cerebellar fibres of the lateral columns are medullated" (Ross). It would appear, therefore, that the latter are the more primitive structures, and that the former are superadded in the cords of the higher animals. The grey matter of the medulla is broken up by changes in the distribution of the white matter into nuclei or masses of nerve-cells, instead of having the crescentic form seen in the spinal cord. These nuclei are connected with the roots of important cranial nerves, and may be regarded as corresponding with the anterior horns of grey matter, with the posterior horns, and with the grey matter between these.

The following nuclei can be found:—(1) the *hypoglossal* nucleus, for the hypoglossal nerve, the motor nerve of the tongue; (2) a *common* nucleus, for a portion of the spinal accessory, vagus, and glosso-pharyngeal nerves; (3) the *principal* or *lower auditory* nucleus, for the auditory nerve; (4) nuclei for the *sixth* or *abducent* nerve, supplying the external rectus muscle of the eye; (5) nucleus for the *fourth* nerve, supplying the superior oblique muscle of the eye; (6) the *facial* nerve, the motor nerve of the face; (7) the *corpus dentatum of the olivary body*, not directly connected with the roots of nerves, but containing nerve-cells. Some fibres, both of the sensory and motor roots of the *fifth* nerve, originate also as far back as the medulla. The third, fourth, sixth, and hypoglossal nerves belong to the system of anterior motor nerves, related to the anterior cornua, whilst the spinal accessory, vagus, glosso-pharyngeal, and fifth belong to the "mixed lateral system,"—that is, they are related to the posterior cornua and intermediate grey matter.

Like the spinal cord, the medulla may be regarded as containing tracts for sensory and motor transmission, and as constituting a series of reflex centres for special movements.

Motor and sensory transmission by medulla.

1. *As a Conductor of Motor and Sensory Impressions.*—Inasmuch also, as such movements as those of the circulation, respiration, and vaso-motor action are necessary to life, destruction of the medulla causes almost instant death. Motor fibres coming from the brain above decussate in the anterior pyramids and then run down the lateral columns of the cord, issuing to the muscles by the anterior roots of the spinal nerves. Hence, whilst section of an antero-lateral column of the cord will cause paralysis of motion on the same side, section of an anterior pyramid above the decussation causes paralysis of motion on the *opposite* side. But fibres carrying sensory impressions also decussate in the grey matter at the bottom of the posterior median fissure of the cord. It follows, therefore, that disease, such as rupture of a vessel causing a clot in the brain, say in the left corpus striatum and left optic thalamus, causes paralysis both of motion and of sensation on the opposite side,—that is, in the case supposed, there would be right hemiplegia. The path of sensory impressions is probably in the grey matter but the precise course of sensory fibres has not been traced.

Medulla as reflex centre.

2. *As a Reflex Centre.*—Numerous special centres have been referred to the medulla oblongata.

(1) *Respiratory* centres, two in number, expiratory and inspiratory, connected with the roots of the pneumogastric nerves. Destruction at once causes cessation of respiratory movements. (2) *Vaso-motor* centre, regulating the calibre of the smaller blood-vessels throughout the body (see p. 30). (3) *Cardiac* centres, probably two in number—one accelerating, associated with the sympathetic; the other inhibitory, connected with the pneumogastric (see p. 29). (4) Centres for *deglutition*, associated with the sensory and motor nerves involved in this process (see NUTRITION, vol. xvii. p. 670). (5) Centre for *voice*, regulating to some extent, through the sterno-cleido-mastoid muscle, the emission of air through the glottis in expiration and phonation. (6) Centre influencing *glycogenesis*, probably by the action of the vaso-motor centre on the blood-vessels of the liver (see NUTRITION, vol. xvii. p. 682). (7) Centre directly influencing *salivary secretion*, from which originate those fibres of the facial, forming the chorda tympani and lesser superficial petrosal, distributed to the salivary glands (see NUTRITION, vol. xvii. p. 672). (8) Centre for the *motor fibres supplying the face and muscles of mastication*. These exist in the facial for the muscles of the face and in the motor portion of the fifth for the muscles of mastication. Further, the medulla receives nervous influences from the higher centres, by which all the centres above enumerated may be more or less influenced.

Pons Varolii.

Pons Varolii.—The pons Varolii is above and in front of the medulla oblongata, and between the hemispheres of the cerebellum. It consists of fibres passing in two directions, viz., longitudinally, connecting the brain above with the medulla and cord below; and transversely, connecting the lateral hemispheres of the cerebellum, thus forming the middle peduncles of that organ. Its general position and appearance are seen in fig. 23. Mixed up with these fibres are various nuclei of grey matter connected with the roots of cranial nerves. The most important of these nuclei are—(1) the nucleus of the facial nerve; (2) the motor nucleus of the fifth nerve; (3) the upper sensory nucleus of the fifth nerve; (4) the inner or chief nucleus of the auditory nerve; (5) the outer or superior nucleus of the auditory nerve; (6) the accessory nucleus of the auditory nerve; (7) the nucleus of the sixth nerve. It will be observed that several of these nerves are also connected with nuclei in the medulla oblongata. Like the cord and medulla, the pons is to be regarded as a conductor of impressions and probably also as a reflex centre. Motor transmission occurs chiefly in the anterior part. As the fibres of the facial nerve decussate in the pons, and then carry influences outwards, unilateral injury or disease of the pons may cause paralysis of the face on the same side as the disease, and paralysis of the limbs on the opposite side if the disease has affected the facial *before* its decussation in the pons. Usually in cases of paralysis of one side (hemiplegia) from a clot or disorganization in one corpus striatum the paralysis of the face is on the same side as that of the limbs. In diseases of the pons loss of sensibility is a much more

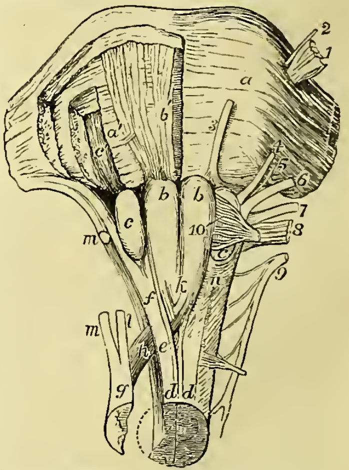

FIG. 23.—Section of medulla oblongata and pons to show the course of fibres. *a*, superficial, and *a'*, deep transverse fibres of pons; *b*, *b*, anterior pyramids ascending at *b'* through pons; *c*, *c*, olivary bodies; *c'*, olivary fasciculus in pons; *d*, *d*, anterior columns of cord; *e*, inner part of right column joining anterior pyramid; *f*, outer part going to olivary fasciculus; *g*, lateral column of cord; *h*, the part which decussates at *k*, the decussation of the pyramids; *l*, the part which joins the restiform body; *m*, that which forms the fasciculus teres; *n*, arciform fibres. 1 and 2, sensory and motor roots of the fifth nerve; 3, sixth nerve; 4, portio dura; 5, portio intermedia; 6, portio mollis of the seventh nerve; 7, glosso-pharyngeal; 8, pneumogastric; 9, spinal accessory; 10, hypoglossal nerve.

rare result than loss of motion, and is always on the opposite side. According to Brown-Séquard, tactile, thermal, and painful impressions pass through the central part of the pons. The numerous centres in the pons are associated in complex reflex movements. Nothnagel has described it as a convulsive centre, because irritation caused severe cramps, but this was no doubt due to irritation of the motor strands passing through it.

Cerebral peduncles.

Cerebral Peduncles.—These contain both sensory and motor fibres, and they establish a connexion between the cerebellum and the cerebrum, and also between the ganglia at the base,—corpora striata, optic thalami, and corpora quadrigemina on the one hand, and the pons and medulla on the other. Little is known of their functions except that they are conductors. Destruction of one peduncle causes the animal to move to the side opposite the lesion, describing a circle somewhat in the manner of a horse in a circus. Irritation may cause pain or movements of various groups of muscles.

Basal ganglia.

Basal Ganglia.—As already shown in tracing the development of the cerebro-spinal system, the brain consists of a series of ganglia, in pairs, more or less overlapped by the cerebral hemispheres. These ganglia, termed the "basal ganglia," are usually held to include, from behind forwards, the corpora quadrigemina, the optic thalami, and the corpora striata; but in addition there are bodies meriting an equal amount of attention, inasmuch as they cannot be regarded as belonging to the cerebral hemispheres. These are the locus niger, the red nucleus of the tegmentum, and the corpora geniculata; but we have no knowledge of their functions. No doubt all these ganglia act along with the cerebral hemispheres, so that practically the whole mass forms one organ.

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uadri-
emina.

Corpora Quadrigemina.—These are two pairs of rounded bodies found above the Sylvian aqueduct, which passes between the third and fourth ventricles. They are situated behind the optic thalami, and are intimately related to the crura, and through these to the pons, medulla, and cord. Homologous with the optic lobes seen in the brain of the fish, frog, and bird (see figs. 17 and 18), and in marsupials and monotremes, their relative size to the mass of the encephalon is much less in the brain of man and of the higher animals. These bodies contain grey matter, covered by a thin stratum of white matter. The two posterior bodies are probably connected with the cerebellum by the superior peduncles of that organ; at all events these peduncles disappear under the base of the corpora quadrigemina. The two posterior bodies are also related to the crura cerebri by the prominences on the sides of the crura known as the inner geniculate bodies. Both anterior and posterior bodies, more especially the anterior, are connected with the optic tracts, and finally, the two anterior bodies unite with the optic thalami. (See fig. 24 below; also, plate XVIII., vol. i., fig. 1, *g, g.*) As shown by their anatomical connexions, the corpora quadrigemina are part of the mechanism of vision. Destruction causes immediate blindness. If, in a pigeon, the encephalon be removed with the exception of these bodies, the iris will still continue to contract on the influence of light. On then destroying one of these bodies, the iris is immobile, and the power of accommodation is lost. As the third cranial nerve (which is known to contain fibres controlling the circular fibres of the iris by which the pupil contracts, and the fibres governing the ciliary muscle by which the eye is accommodated or focused to varying distances) originates in the grey matter of the floor of the Sylvian aqueduct, close to the corpora quadrigemina, it is held that these bodies are the centres of the reflex movements of the iris and of the ciliary muscle. The corpora quadrigemina are also the first recipients of visual impressions. When light falls on the retina changes are there induced which stimulate the optic nerve-fibres, and these fibres carry impressions through the optic tracts to the corpora quadrigemina. What then occurs is matter of conjecture. Whether sensation is there excited, or whether to produce sensation it is necessary that the impulses be sent onwards to the cerebrum, or whether the impressions directly received from the retina may excite, through the corpora quadrigemina and adjacent ganglia, reflex movements (like those of the somnambulist, who may see so that his steps are taken rightly, but who may at the same time not see consciously), are all speculative questions. We know that these bodies are concerned in the movements of the iris and of the ciliary muscle, but their great proportionate size in lowly-formed brains indicates that this is probably a secondary function, and that they are largely concerned in the phenomena of consciousness of light and colour.

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lami.

Optic Thalami.—These are two ganglionic masses placed behind the corpora striata and in front of the corpora quadrigemina. The internal surfaces are seen chiefly in the third ventricle, the upper surfaces in the same ventricle and the lateral ventricles (see vol. i. pp. 875, 876, figs. 74 and 75), whilst the external and under surface of each thalamus is united with other parts of the brain. The under surface receives fibres from the crus cerebri, whilst the upper surface is covered by fibres which diverge and pass between the thalamus and a mass of grey matter in the extra-ventricular portion of the corpus striatum (called lenticular nucleus), to form a white layer called the "internal capsule." From the internal capsule, which thus contains fibres from the optic thalamus, fibres radiate outwards to the surface of the cerebral hemispheres. The under surface of the thalamus is connected with the tegmentum,—that is, with the layer of fibres forming the upper surface of the crus cerebri. They also receive fibres from the corpora quadrigemina, and according to some authorities from the superior peduncles of the cerebellum. The substance of the thalamus contains nerve-cells, scattered and also aggregated into two nuclear masses, but the relations of these to nerve-tracts have not been ascertained. It is important physiologically to notice that the thalami receive fibres from the back of the crura, and therefore are probably related to the posterior or sensory portion of the spinal cord.

There is still much uncertainty as to the functions of the optic thalami. The most commonly received opinion is that they are centres for the reception of peripheral impulses, which they may elaborate and transmit forwards to the corpora striata, or directly to the cerebral hemispheres. If the sensory impulses received by the optic thalami are sent to the corpora striata, and by these transmitted downwards and outwards through the crura cerebri, then reflex actions may occur in which the basal ganglia are the centres; but, if the impulses are sent up, in the first place, to the cerebral hemispheres, and by these transmitted down to the corpora striata, then the action must include the higher mechanism of the grey matter of the hemispheres. In the first case it is supposed by those who hold that consciousness is specially connected with the grey matter of the hemispheres that the action would be purely reflex and unconscious. Experiment has not thrown much light on this problem, owing to the deep-seated situation of these bodies rendering the results of operative interference untrustworthy. The little that has been done shows that injury to them does not cause paralysis of motion. Nor can it be said that such injuries cause loss of sensation, the only phenomenon observed being that the animal places its limbs in anomalous positions, and does not seem to be aware of having done so. Meynert is of opinion that the optic thalami fulfil the same functions as to tactile impressions—that is, impressions on the periphery of the body—that the corpora quadrigemina do for visual impressions—that is, impressions on the retina. In cases of apoplexy in which these bodies are involved there are always sensory disturbances on the side opposite the lesion. This would lead to the inference that the optic thalami are the sensory ganglia of the opposite sides of the body. They are not, however, the first ganglionic apparatus through which sensory impressions pass, but they probably co-ordinate in some way centripetal impulses before these are sent to the cerebral hemispheres, where they are correlated with feeling. Further, as the old name "optic thalami" indicates, these ganglia are concerned in some way in vision, because, if seriously injured, blindness, or at all events disturbance of vision, is one of the constant results. This favours the view that they are the "middlemen" between special sensory centres and the higher centres of the cerebrum.

Corpora striata.

Corpora Striata.—These ganglia, sometimes termed the "ganglia of the cerebral hemispheres," situated in front and on the outer side of the optic thalami, are seen in the lateral ventricles. (See vol. i. pp. 875, 876, figs. 74 and 75.) The greater part of each is imbedded in the white substance of the hemisphere (extra-ventricular portion), whilst the part seen in the floor of the lateral ventricle is called the intra-ventricular portion. Each of these contains a nucleus of grey matter, the *nucleus caudatus* in the intra-ventricular and the *nucleus lenticularis* in the extra-ventricular. The latter is separated internally from the intra-ventricular portion by a layer of white matter called the "internal capsule," whilst on the outer side there is another layer of white matter called the "external capsule," beyond which, again, is a lamina or web of grey matter, called the "claustrum," which separates the external capsule from the island of Reil. The internal capsule is of great importance inasmuch as it is continuous with the *crusta*, a portion of the crus cerebri, which, in turn, is a continuation of the pyramidal fibres of the medulla oblongata and the pons. Multipolar nerve-cells are found in the nucleus caudatus; in the claustrum the cells are small and spindle-shaped. Posteriorly, therefore, the corpus striatum is related by fibres with the optic thalamus; inferiorly, through the internal capsule, with the pyramidal portion of the medulla and cord; and externally and superiorly with the grey matter of the cerebrum. The corpus striatum is a centre for the co-ordination of centrifugal or motor impulses. It may be roused into activity by impressions reaching it directly from the optic thalamus, but probably it usually acts in obedience to impulses coming from the cerebral hemispheres. When a clot of blood is formed in, say, the right corpus striatum there is motor paralysis of the opposite side of the body, and, according to the size of the clot, the paralysis may affect more or less completely the different groups of muscles. Destruction of the two bodies destroys voluntary movement, but the animal may move forwards as in running. Destruction of the nucleus caudatus renders movements of progression impossible, and the animal performs movements of rotation. Nothnagel by injecting a minute drop of a solution of chromic acid destroyed the nucleus lenticularis of a rabbit, with the result of throwing the animal into complete unconsciousness. He also states that in the corpus striatum of the same animal there is a point, the *nodus cursorius*, the excitation of which caused the rabbit to rush forwards. This observation agrees with the statement of Magendie that, when he injured the corpora striata, the animal seemed to have an irresistible propulsion forwards. Ferrier states that when the corpora striata were stimulated by an interrupted current convulsive movements of the opposite side of the body took place; and when the current was powerful the side of the body opposite to the side of the brain stimulated was forcibly drawn into an arch.

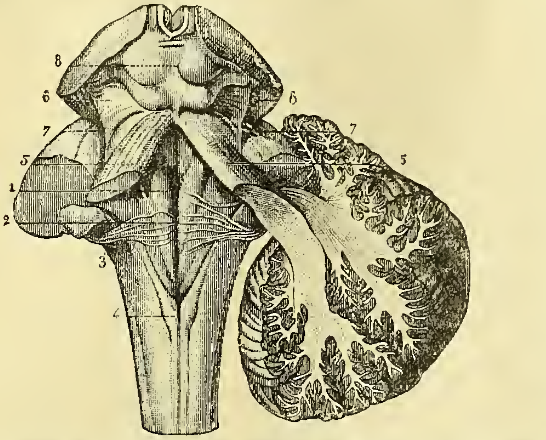

FIG. 24.—Three pairs of cerebellar peduncles (from Sappey, after Hirschfeld and Leveillé. Quain). On the left the three cerebellar peduncles have been cut short; on the right side the hemisphere has been cut obliquely to show its connexion with the superior and inferior peduncles. 1, median groove of fourth ventricle; 2, the same groove at the place where the auditory striæ emerge from it to cross the floor of the ventricle; 3, inferior peduncle or restiform body; 4, funiculus gracilis; 5, 5, superior peduncles,—on the right the dissection shows the superior and inferior peduncles crossing each other as they pass into the white substance of cerebellum; 6, 6, fillets at the side of crura cerebri; 7, lateral grooves of crura cerebri; 8, corpora quadrigemina.

Peduncles of cerebellum.

Cerebellum.—In connexion with the physiology of this organ it is important to note its connexions with the rest of the cerebro-spinal axis. It has three peduncles: (1) the superior peduncles (see fig. 24)—crura ad cerebrum, or processes ad testes—together with the valve of Vieussens, connect the cerebellum to the cerebrum; (2) the inferior peduncles, or crura ad medullam, are the superior extremities of the restiform bodies; (3) the middle peduncles, or crura ad pontem, much the largest, are the lateral extremities of the transverse fibres of the pons Varolii. They act as commissural fibres for the hemispheres of the cerebellum. All these peduncles pass into the interior of the cerebellum at its forepart. In the interior of the organ, where the peduncles enter, we find a nucleus of grey matter, the *corpus dentatum*. The cortical substance consists of two layers,—an outer *molecular* layer, consisting of a delicate matrix containing a few round cells and fibres, and an inner or *granule* layer, containing granules or nucleated corpuscles closely packed together. The corpuscles are from $\frac{1}{4000}$th to $\frac{1}{2500}$th of an inch in diameter, and are mixed with a network of delicate nerve-fibres. At the junction of the granular layer with the molecular layer there are peculiar large cells called "Purkinje's cells." They are flask-shaped and about $\frac{1}{800}$th to $\frac{1}{1000}$th of an inch in diameter, and the long process is directed towards the surface of the cerebellum (see fig. 25). The white centre of each lamina consists of delicate nerve-fibres, the terminations of which have not been satisfactorily made out. Probably they end in the plexus of nerve-fibres in the granule layer, or in the processes of Purkinje's cells. On comparing the section of cerebrum (fig. 28) with that of cerebellum (fig. 25) the contrast is striking. The structure of cerebellum is more like that of the retina (vol. i. p. 888, fig. 78) than of any other nerve-centre.

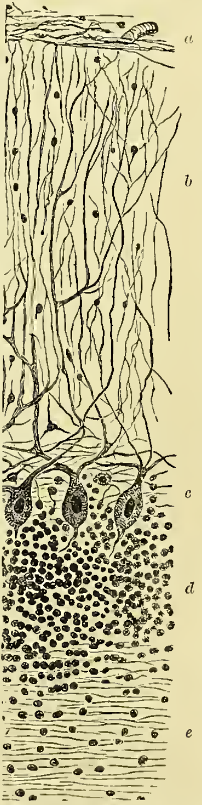

FIG. 25.—Vertical section through cortex of cerebellum (Sankey). *a*, pia mater; *b*, external layer; *c*, layer of cells of Purkinje; *d*, inner or granule layer; *e*, medullary centre.

Experiments on cerebellum.

Results of Experiments.—The cerebellum is insensible to mechanical excitations. Puncture causes no indications of pain, but there may be twisting of the head to the side. Ferrier states that Faradaic irritation causes movements of the eyeballs and other movements indicative of vertigo. Section of the middle peduncle on one side causes the animal to roll rapidly round its longitudinal axis, the rotation being towards the side operated on.

If the cerebellum be removed gradually by successive slices—an operation easily done in a pigeon—there is a progressive effect on locomotive actions. On taking away only the upper layer there is some weakness and a hesitation in gait. When the sections have reached the middle of the organ the animal staggers much, and assists itself by its wings in walking. The sections being continued further, it is no longer able to preserve its equilibrium without the assistance of its wings and tail; its attempts to fly or walk resemble the fruitless efforts of a nestling, and the slightest touch knocks it over. At last, when the whole cerebellum is removed, it cannot support itself even with the aid of its wings and tail; it makes violent efforts to rise, but only rolls up and down; then, fatigued with struggling, it remains for a few seconds at rest on its back or abdomen, and then again commences its vain struggles to rise and walk. Yet all the while sight and hearing are perfect. See fig. 26. It attempts to escape, and appears to have all its sensations perfect. The results contrast very strongly with those of removing the cerebral lobes. "Take two pigeons," says Longet; "from one remove completely the cerebral lobes, and from the other only half the cerebellum; the next day the first will be firm on its feet, the second will exhibit the unsteady and uncertain gait of drunkenness."

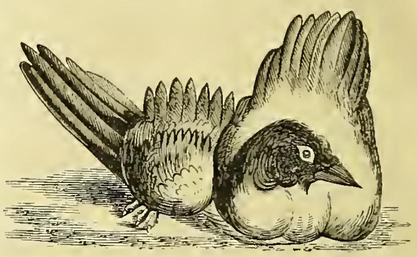

FIG. 26.—Pigeon from which the cerebellum has been removed.

There is thus a loss of the power of co-ordination, or of regulation of movement, without the loss of sensibility, and hence it has been assumed that in some way or other the cerebellum acts as the co-ordinator of movements.

Co-ordination of movement.

Co-ordination of Movement.—The nervous mechanisms by which movements are co-ordinated—that is, adapted to specific ends—are not thoroughly understood, but a short description of what is known may be here given. Muscular movements may be either simple or complex. In winking, the movement of the eyelid is effected by two muscles, one bringing the lid down, the other raising it. But picking up a pen from the table, taking a dip of ink, and writing a few words involve a complicated set of movements of the muscles of the trunk, shoulder, arm, forearm, fingers, and thumb. To perform the movements with precision each muscle or group of muscles must act at the right time and to the proper amount. It is also clear that all this is accomplished automatically. We are not conscious of the requisite combinations; but it must be noted that many of these complicated movements are first acquired by conscious efforts, and that they become automatic only by repetition. Again, in walking, equilibrium is maintained by a delicate series of muscular adjustments. When we swing forward one leg and balance the body on the other many muscular movements occur, and with every change in the position of the centre of gravity in the body there are corresponding adjustments. It would appear that in all mechanisms of co-ordination the first part of the process is the transmission of sensory impressions from the periphery. These sensory impressions may be derived from the skin or muscles, and may be caused by variations of pressure arising in them. Thus, if we lift a heavy weight, as a large stone, by the right hand and raise it to the bend of the elbow we throw the body to the other side by the action of the muscles of that side, thus maintaining the equilibrium. We judge of the amount of force necessary to overcome an obstruction by the feeling of resistance we encounter. All the movements of the body, therefore, give rise to feelings of varying pressures, and these feelings regulate the amount or degree of muscular action necessary to maintain equilibrium, or to perform a requisite movement. This is at first a conscious experience, and a child has to pass through an education, often involving pain, before the nervous mechanisms become automatic and the movement is done without effort. But the ordinary sensory nerves, coming from skin and muscle, are not the only channels by which such guiding mechanisms are set in action. As one would expect, sensory impressions, such as those associated with sight and hearing, may be brought into play.

Impressions from semicircular canals.

1. *Peripheral Impressions from Semicircular Canals.*—If the membranous portion of the horizontal semicircular canal in the internal ear of a pigeon be cut, the bird moves its head from side to side, and if one of the vertical canals be divided it moves the head up and down. The effects may pass off in a few days if only one canal has been cut. If the canals on both sides be divided the movements are exaggerated and the condition becomes permanent. It will then be observed that the animal has lost the power of co-ordinating its movements. It can rest with only a twitching, perhaps, of the head, but if it attempt to fly or walk its movements are indefinite and irregular, like those of a dizzy person, or like those described as following injury to the cerebellum. The irregular movements do not arise from deafness, or noises in the ears, or partial paralysis, or from an uncontrollable impulse. Any strong sensory

impression, such as holding the bird, supporting its beak, or holding a brilliant light before its eyes, will steady it, and it has been noticed that "it can, even without assistance, clean its feathers and scratch its head, its beak and foot being in these operations guided by contact with its own body." It has been supposed that the semicircular canals are concerned in the mechanism of equibration, —a view urged chiefly by Mach and Crum-Brown. If a blindfolded man is seated on a horizontal rotating table, such as that used in a lighthouse for rotating or eclipsing the light, and the table is turned round, at first there is a sensation of movement in the same direction as that of the table; then this sensation fades away, until he has no sensation of movement, although the table may be rapidly rotating; finally, if the table be stopped without a jerk there is first a very short period in which there is no definite sensation, which is succeeded by a sense of rapid movement in the opposite direction, often accompanied by a feeling of nausea. Now it is evident that neither sight nor touch nor muscular sensations can give a sense of rotation in these circumstances, and yet it is possible to form a fairly accurate judgment of the angle through which the body has moved. It has been suggested that this is effected by the action of the semicircular canals. The membranous portions are surrounded by a fluid called the "endolymph," and are free to move through a short distance. Hence it has been supposed that rotations more or less rapid must cause variations of tension of the membranous portion. Thus, if the membranous part, especially the ampulla or dilated ends of the canals, lag behind when rotation in one direction takes place, the nerves ending in them will be subjected to a strain; by and by both membranous portions and surrounding parts will be moving with the same velocity, when there will be no strain and no sense of movement; and at last, when the rotatory movement is arrested, there will be a tendency on the part of the membranous portions, as they are floating in a fluid, to move on a little farther than the rest, and thus again produce a strain, causing a sensation of movement in the opposite direction. By similar reasoning it can be shown that if we take the peculiar position of the three canals into consideration any movement in space might be thus appreciated, and these appreciations enter into the judgment we form of the movements. According to this theory, the sense of equilibrium may be largely due to impressions derived from the position of the head, and, as muscular movements required for placing the body in definite positions are determined, as we have seen, by peripheral impressions, the irregular movements of the pigeon, after injury to these canals, may be accounted for. It is not improbable that in the bird, which from the structure of its extremities—feet and wings—can have no peripheral impressions so delicate as those derived from the papillæ of the skin on the extremities of other animals, the sense of equilibrium is maintained chiefly by impressions from these canals, and this may account for the comparatively large size of these organs in birds and fishes. This is in correspondence also with the requirements of birds in the balancings of flight and of fishes in swimming. It is well known that disease or injury of these canals in the human being produces symptoms of vertigo and a diminution of the power of co-ordinated action, as in Menière's disease, showing that the canals, even in man, have similar functions to those in the bird.

npres-
ons
om eye.

2. *Peripheral Impressions from the Eye.*—Many movements are guided and controlled by the sense of vision. Simply blindfolding a bird usually makes it passive, and it will not attempt either to walk or to fly; the same effects to a less degree may be seen in a mammal; and a blindfolded man will stagger in his gait. The wonderfully accurate movements of the blind in walking are acquired by long and laborious effort, and are guided by the sensations of hearing, of touch, and of resistance. If the optic lobes of a frog be destroyed, its power of balancing itself is lost. There are thus at least three channels by which peripheral impressions pass to the centres and seem to guide or co-ordinate movement: (1) from the periphery, by nerves of ordinary sensibility arising in the skin, muscles, and viscera; (2) from the semicircular canals of the ear, by special nerve-fibres in the auditory nerve; (3) from the eye, by fibres of the optic nerve. How and where these skeins of sensitive impressions are gathered up and so arranged as to call forth the requisite movements can only be conjectured; but the cerebellum is the organ most likely to be concerned in such a mechanism. It is in organic connexion with many of the nerve-fibres conveying sensory impressions. By the restiform bodies it receives many of the sensory fibres of the spinal cord; the auditory nerve has roots intimately related to the cerebellum; and it is fair to assume that there are communications between the corpora quadrigemina and the cerebellum. Stimulation of the cerebellum causes movements of the eyeballs, and disease of the cerebellum is sometimes attended by blindness. How the cerebellum co-ordinates movement is quite unknown, and the difficulty in explaining its functions is not lessened by the clinical fact that extensive disease of this organ may exist without any appreciable sensory or motor disturbance. There is no evidence to support the view of the founders of phrenology that the cerebellum has to do with the sexual functions.

Cerebral Hemispheres.—As these have been fully described in vol. i. p. 873, it is only necessary here to point out the anatomical facts that assist in explaining the functions of the organ. It is important to observe, first, the general arrangements of the fibres, and, secondly, the arrangement and structure of the grey matter. The white matter of the cerebrum consists of ascending or peduncular fibres, longitudinal or collateral fibres, and of transverse or commissural fibres.

Peduncular fibres of cerebrum.

(1.) *Peduncular Fibres.*—The crusta of the cerebral peduncles consists of bundles of longitudinal fibres derived mainly from the anterior pyramid of the medulla. The crust is quadrilateral in form, but in ascending to the hemispheres it becomes flattened from above downwards, so that the fibres spread out like a fan. The fan formed by these fibres is bent into the form of an incomplete hollow cone, the convex surface of which is directed upwards and inwards. Thus the fibres pass between the optic thalamus and the lenticular nucleus, forming the internal capsule. Higher up the fibres pursue their course beneath and to the outside of the thalamus and the caudate nucleus, and over the lenticular nucleus. "Still higher up the internal capsule has spread out from before backwards, while the anterior half forms an obtuse angle with the posterior. The angle where the halves meet is called the knee (fig. 27, K), while the divisions themselves are called the anterior (fig. 27, IK′) and posterior segments of the internal capsule" (Ross). On emerging from the basal ganglia the fibres of the internal capsule radiate in all directions to reach the cortex of the brain, giving rise to the appearance called the "corona radiata." The following sets of fibres have been traced into connexion with the cerebrum.

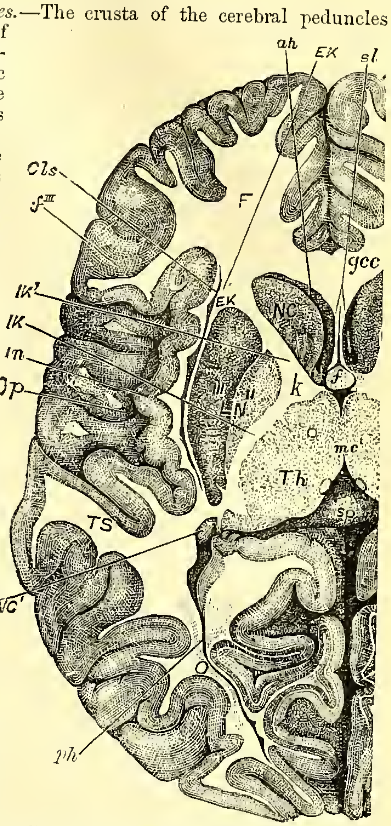

Fig. 27.—(After Flechsig.) Horizontal section of brain of child nine months old, only a portion of the right side being shown. *F*, frontal, *TS*, temporo-sphenoidal, and *O*, occipital lobes; *op*, operculum; *In*, island of Reil; *Cls*, claustrum; *f‴*, third frontal convolution; *Th*, optic thalamus; *NC*, caudate nucleus; *NC′*, tail of caudate nucleus; *LN*, lenticular nucleus; *II,III*, second and third divisions of lenticular nucleus; *EK*, external capsule; *IK*, posterior division, *IK′*, anterior division, and *K*, knee of internal capsule; *ah*, *ph*, anterior and posterior horns respectively of lateral ventricles; *gcc*, knee of corpus callosum; *sp*, splenium; *mc*, middle commissure; *f*, fornix; *sl*, septum lucidum.

(*a*) Sensory peduncular fibres, derived from the posterior root-zones and the columns of Goll. These are in connexion with the cerebellum; but, as shown by Meynert, Flechsig, and others, many pass up through the pons to reach the crus cerebri, occupying the posterior and external portion of the pyramidal tract. They do not appear to be connected with the optic thalamus and the lenticular nucleus, but pass between them to the cortex. (*b*) Fibres from the roots of the optic nerves, reaching the brain by what have been called the "optic radiations of Gratiolet." This bundle of fibres issues from the posterior and external border of the optic thalamus and is closely applied to the peduncular sensory tract in its passage through the internal capsule, and the fibres seem to be connected with the convolutions of the occipital lobe. It is important to note that at least one of the roots of the optic nerve (the internal) passes into the external geniculate body and thence into the anterior bodies of the corpora quadrigemina. Thus there is a path for the passage of impressions from the retina to the cortex of the brain. (*c*) Fibres from the olfactory lobes have been traced to a junction with the optic radiations of Gratiolet, and pass with them to the convolutions of the cortex of the occipital or temporo-sphenoidal lobe. (*d*) The pyramidal tract has already been traced through the spinal cord, medulla, and pons. It then goes on, as already seen, to form the internal capsule and the corona radiata, the fibres ending in the parietal lobule, the paracentral lobule, the superior extremities of the ascending frontal and parietal convolutions, probably the posterior extremity of the first frontal convolution, the posterior extremity of the third frontal, and the inferior extremities of the ascending frontal and parietal convolutions,—in short, in the convolutions forming the middle and parietal region of the surface of the cortex. (*e*) Fibres issuing from the external surface of the optic thalamus to join the internal capsule. These are distributed to the convolutions of the frontal and parietal lobes. (*f*) Fibres issuing from the external surface of the caudate nucleus, passing also into the corona radiata. (*g*) Fibres issuing from the superior and internal surface of the lenticular nucleus to join the ascending fibres of the internal capsule. (*h*) Fibres ascending from the superior peduncle of the cerebellum. Flechsig says that some of the fibres of the superior peduncle of the cerebellum of the opposite side pass uninterruptedly through the red nucleus and along the internal surface of the fibres of the pyramidal tract to be distributed to the central convolutions of the cerebrum. (*i*) Fibres issuing from the corpus callosum and descending into the internal capsule. (*k*) Fibres of the external capsule which ascend from the crusta and ultimately reach the cortex through the corona radiata.

In addition to the peduncular fibres above enumerated, all of which belong to what may be termed the system of the internal capsule and corona radiata, fibres from the fornix, tænia semicircularis, outer layer of septum lucidum, and the fillet of the crus also pass from below upwards to the cortex of the hemispheres (Ross).

Longitudinal fibres of cerebrum.

(2.) *Longitudinal or Collateral Fibres.*—(*a*) Fibres running immediately below the surface of the cortex, and connecting the grey matter of adjacent convolutions. (*b*) Fibres in the gyrus fornicatus, a convolution immediately above the corpus callosum. It is said that bands of these fibres arise in the anterior perforated space and pass completely round the corpus callosum to end in the same perforated space, and that offsets of these fibres pass upwards and backwards to reach the summits of the secondary convolutions derived from the gyrus fornicatus near the longitudinal fissure. (*c*) Longitudinal fibres of the corpus callosum (nerves of Lancisi), connecting the anterior and posterior ends of the callosal convolution. (*d*) Longitudinal septal fibres, lying on the inner surface of the septum lucidum, and entering into the gyrus fornicatus. (*e*) The fasciculus uncinatus, passing across the bottom of the Sylvian fissure and connecting the convolutions of the frontal and temporo-sphenoidal lobes. (*f*) The longitudinal inferior fasciculus, connecting the convolutions of the occipital with those of the temporal lobe.

Commissural fibres of cerebrum.

(3.) *Transverse or Commissural Fibres.*—(*a*) Many, if not all, of the fibres of the corpus callosum pass transversely from one side to the other and connect corresponding convolutions in the hemispheres. This is the generally accepted view; but Professor Hamilton of Aberdeen has recently stated that his preparations show that there is no such commissural system between convolutions, and that the fibres decussating in the corpus callosum are not continued to convolutions on the other side, but pass downwards. (*b*) The fibres of the anterior commissure wind backwards through the lenticular nuclei to reach the convolutions round the Sylvian fissure. (*c*) The fibres of the posterior commissure run through the optic thalami.[1]

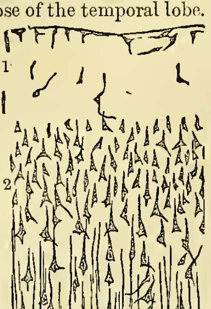

Fig. 28.—(After Meynert.) Vertical section of a furrow of third cerebral convolution of man. 1, layer of scattered small cortical corpuscles; 2, layer of close-set small pyramidal corpuscles; 3, layer of large pyramidal cortical corpuscles; 4, layer of small close-set irregular-shaped corpuscles; 5, layer of fusiform corpuscles (like those in the claustrum); *m*, medullary lamina.

Arrangement and structure of grey matter.

Arrangement and Structure of Grey Matter.—The grey matter in the medulla and basal ganglia has been already considered. A web or sheet of it is also thrown over the surface of the cerebrum, and forms the outer portion of all the convolutions. The cortical substance consists of cells and fibres imbedded in a matrix similar to the neuroglia of the spinal cord. It may be divided into five layers, which merge into each other by almost insensible gradations. The most external layer consists of delicate nerve-fibres, neuroglia, and a few small round cells destitute of processes (see fig. 28). Going deeper we find cells of a characteristic pyramidal form, the largest being in the deepest layer. Their bases are turned inwards, and their apices towards the surface of the convolution. Cleland states that fibres passing from the apices are continuous with the delicate fibres found on the very surface of the cortex. In the ascending frontal convolutions Betz and Mierzejewski have found pyramidal cells two or three times larger than those of other regions of the cortex, and these have been termed "giant-cells." All the pyramidal cells, no doubt, anastomose by their processes, and give origin to the nerve-fibres of the white substance, but it is rarely possible to trace the fibres from cell to cell. A consideration of these anatomical facts, along with those mentioned in connexion with the comparative anatomy of the brain, shows that the cerebral hemispheres are in intimate connexion by fibres with all the other portions of the cerebro-spinal system. Further, they are not only intricate in structure themselves, but the commissural sets of fibres indicate that there is harmony of function between one part and another. In determining the function of so complicated an apparatus recourse must be had to the evidence (1) of development, (2) of comparative anatomy, (3) of human anatomy, (4) of the observed effects of disease before and after death, and (5) of experiment. Facts have already been collected from the first three of these fields of inquiry, all tending to show that the grey matter of the hemisphere is associated with the manifestation of intelligence in its various forms. The phenomena of disease support the same conclusion. Diseases producing slow changes in the layer of grey matter on the cortex are invariably associated with mental disturbance, such as melancholia, mania, or dementia. If the grey matter be suddenly injured or submitted to compression, as by a blow causing fracture and depression of a portion of the skull, or the effusion of fluid consequent on inflammation, unconsciousness is a certain result. So long as the pressure continues there is no consciousness; if it be removed, consciousness may soon return. On the other hand, if the disease affect the white matter of the central portions or the ganglia at the base, there may be paralysis or convulsions without consciousness being affected. All the facts, therefore, of pathology relating to the brain indicate that the grey matter on the surface of the hemispheres is the organ of consciousness and of all mental operations. This statement is now an axiom of medical science, and the basis of the rational treatment of the insane and of all maladies of the central nervous organs.

Two methods of experiment upon the cerebrum have usually been followed, and both have yielded important results.

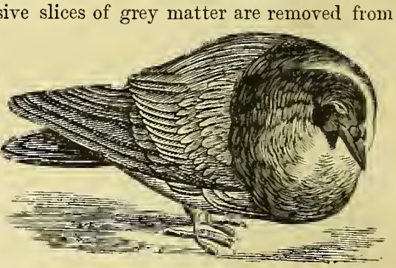

Fig. 29.—Pigeon, in which the cerebrum has been injured or removed.

Removal of grey matter.

(*a.*) *Removal.*—Flourens and the older observers were aware of the fact that as successive slices of grey matter are removed from the surface of the cerebrum an animal becomes more dull and stupid, until at last all indications of perception and volition disappear. A pigeon in this condition (see fig. 29), if carefully fed, may live for many months; to quote from Dalton—

> "The effect of this mutilation is simply to plunge the animal into a state of profound stupor, in which it is almost entirely inattentive to surrounding objects. The bird remains sitting motionless upon his perch or standing upon the ground, with the eyes closed and the head sunk between the shoulders. The plumage is smooth and glossy, but is uniformly expanded by a kind of erection of the feathers, so that the body appears somewhat puffed out, and larger than natural. Occasionally the bird opens its eyes with a vacant stare, stretches its neck, perhaps shakes its bill once or twice, or smooths down the feathers upon its shoulders, and then relapses into its former apathetic condition."

Similar observations have also been made on reptiles and mammals, but the latter survive the operation for a comparatively short time. In watching such an animal it is difficult to divest one's mind of the belief that it still feels and sees and hears. It may be observed that it rarely makes movements unless stimulated from without. Thus it may remain motionless for many hours; but if pushed, or gently touched, it moves. As remarked by Prof. M. Foster—

> "No image, either pleasant or terrible, whether of food or of an enemy, produces any effect on it, other than that of an object reflecting more or less light. And, though the plaintive character of the cry which it gives forth when pinched suggests to the observer the existence of passion, it is probable that is a wrong interpretation of a vocal action; the cry appears plaintive, simply because, in consequence of the completeness of the reflex nervous machinery and the absence of the usual restraints, it is prolonged. The animal is able to execute all its ordinary bodily movements, but in its performance nothing is ever seen to indicate the retention of an educated intelligence."

Electric stimulation of brain-surface.

(*b.*) *Electrical Stimulation of Surface of Brain.*—It is remarkable that, although many of the early workers in cerebral physiology stimulated the surface of the brain by electric currents, they observed no effect, and therefore Magendie, Matteucci, Longet, Weber, Budge, Schiff, and others taught that irritation of the surface of the hemispheres called forth no muscular movements; and it was generally accepted that the grey matter on the cortex of the brain was entirely concerned in the phenomena of sensation, volition, and intellectual action. During the Franco-German war in 1870 Hitzig had occasion to apply galvanism to a portion of the exposed brain of a wounded soldier, and he observed contractions of the muscles of the eyeball. When peace was restored, experiments were made on the lower animals by Hitzig and Fritsch, in which a portion of exposed brain was irritated by a continuous current, and it was observed that the phenomena took place on opening and closing the current. By these experiments the German observers discovered that, when certain areas of grey matter were stimulated, contractions of certain muscles occurred, and they were thus able to map out areas for groups of muscles. Immediately afterwards the research was taken up by Professor David Ferrier of King's College, London, who, using a Faradaic instead of a continuous current, greatly extended the field of inquiry, and obtained many important results, which are not only

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[1] In preparing the foregoing sketch of the fibres of the cerebrum the writer is much indebted to Ross, *Diseases of the Nervous System.*

Ferrier's motor areas.

of value in cerebral physiology but have been successfully applied to the diagnosis of various diseases of the nervous system. The motor areas as determined by Ferrier in the monkey are shown in fig. 30. Dr Ferrier has also indicated the corresponding motor areas in man by carefully comparing the convolutions with those of the monkey.[1] An inspection of the figures shows that the areas which, when stimulated, give rise to definite movements are distributed only over a part of the cortex. As stimulation gives rise to no movements over other regions of the brain, these have been assumed to be connected with psychical states, such as sensation, volition, &c. Much controversy has arisen as to the real nature of these so-called "motor areas." It has been clearly ascertained that the effects are not due to diffusion of the electric currents influencing other parts of the brain. That there is to some extent such diffusion between the electrodes there can be no doubt, but the exact correspondence between the area stimulated and the movements produced, and the fact that shifting the electrodes a very short distance to one side or another is followed by different results, show that the effect is somehow owing to changes excited by the electric current in that particular area of grey matter. Hitzig, Ferrier, and others have also found that removal of the layer of grey matter of a "motor centre" is followed by enfeeblement of the movements assigned to the area, but in the course of a few days the paralytic symptoms disappear. The latter effect cannot be due to the corresponding centre on the opposite side taking up the work "as subsequent destruction of the latter produced the usual paralysis on the side opposite to the lesion, but did not cause a repetition of the paralysis on the side opposed to the first lesion" (Carville and Duret). It would appear, therefore, that after destruction of a centre on one side some other part of the same hemisphere may take up the functions of the destroyed part. Goltz of Strasburg has removed large portions of the grey cortex (even to the extent of almost the whole of one hemisphere) by a jet of water so as to avoid hæmorrhage, and still recovery of motor power took place after a time, although there remained "clumsiness in the execution of certain movements." His opinion is that the paralytic phenomena are caused by the injury exciting an inhibitory action on lower centres. This view, substantially that advocated for many years by Brown-Séquard does not explain why it is that gentle irritation of the centre by a weak Faradaic current calls forth movements of a definite character. The evidence, therefore, is strongly in favour of the view that there are definite motor areas of grey matter on the cortex,—that is, in ordinary circumstances these areas are intimately related to specific muscles or groups of muscles. It is quite possible, however, that each group of muscles does not depend on one area alone, but on several, whilst it is more intimately related to one than to the others. This would account also for the fact that movements of a group of muscles may be excited by stimulation of other areas than those mapped out by Ferrier and Hitzig. Recently areas associated with definite movements of the thorax, abdomen, and pelvis have been discovered by Horsley and Schäfer, and thus almost all the muscular mechanisms have been connected with some of the cerebral convolutions.

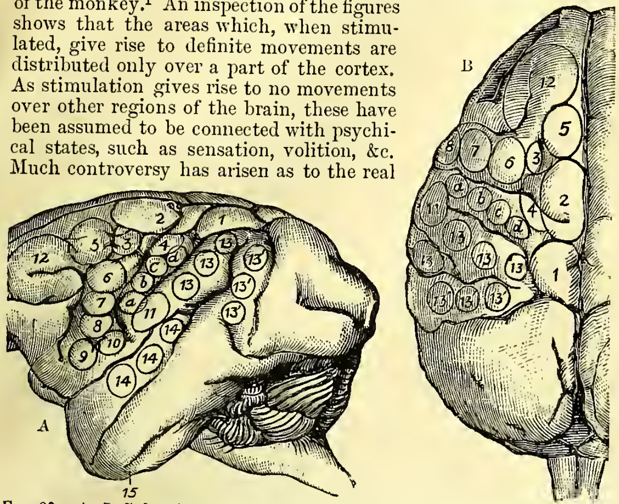

FIG. 30.—A. Left hemisphere of monkey. B. Upper surface of hemisphere of monkey. The numbers in A and B correspond. 1, advance of opposite leg as in walking; 2, complex movements of thigh, leg, and foot, with adapted movements of trunk; 3, movements of tail; 4, retraction and adduction of opposite fore-limb; 5, extension forward of opposite arm and hand, as if to reach or touch something in front; *a*, *b*, *c*, *d*, individual and combined movements of fingers and wrists, ending in clenching of fist; 6, supination and flexion of forearm, by which the hand is raised towards the mouth; 7, action of zygomatics, by which the angle of the mouth is retracted and elevated; 8, elevation of ala of nose and upper lip, with depression of lower lip, so as to expose the canine teeth on the opposite side; 9, opening of mouth with protrusion of tongue; 10, opening of mouth with retraction of tongue; 11, retraction of angle of mouth; 12, eyes opening widely, pupils dilating, head and eyes turning towards opposite side; 13, 13′, eyeballs moving to opposite side,—pupils generally contracting; 14, sudden retraction of opposite ear; 15, subiculum cornu ammonis,– torsion of lip and nostril on same side. (Ferrier.)

Sensory centres.

Ferrier has also attempted to differentiate sensory centres. On stimulating the angular gyrus he obtained movements of the eye and associated movements of the head, and he regarded the phenomena as being "merely reflex movements on the excitation of subjective visual sensation." He then found that, "when the angular gyrus of the left hemisphere was destroyed, the animal was blind on the right eye soon after the operation, but recovered sight completely on the following day." On destroying the angular gyri of both hemispheres, an animal became permanently blind in both eyes. In neither case was there motor paralysis. By similar processes of thought and experiment he placed the auditory centre in the superior temporo-sphenoidal convolution, the centres of taste and smell at the extremity of the temporo-sphenoidal lobe, and that of touch in the gyrus uncinatus and hippocampus major. On the other hand, Goltz asserts that even after removal of a considerable part of the cortex the animal is not actually blind, but suffers from an imperfection of sight; and he states that he "can no more obtain distinct evidence of localization in reference to vision or other sensations than in reference to movements." Ferrier's view is supported by the observations of Munk, who finds that destruction of a considerable portion of the occipital lobes causes blindness. Munk has put forth the important distinction that there may be blindness in the sense of total deprivation of vision, and "psychical blindness," or the "inability to form an intelligent comprehension of the visual impressions received"; and he supposes that the grey matter of the cortex over the occipital lobes has to do with the elaboration of simple visual impressions into perceptions. In like manner he concludes that other parts of the cortex may have to do with the elaboration of tactile, olfactory, gustatory, and auditory sensations. This is a likely hypothesis, and not very dissimilar to what has been held for many years, the only novelty being that there is localization in these actions. At present the question cannot be regarded as settled; but it may be stated generally that the posterior portion of the brain has to do chiefly with the reception of sensory impressions, and the middle and lateral regions with the transmission outwards of motor impulses. But there still remains the anterior portion. Electrical irritation of the præ-frontal region of the cortex in the monkey causes no motor reaction. Complete destruction causes no paralysis of motion and no sensory disturbance. Dr Ferrier states :—

> "Removal or destruction by the cautery of the antero-frontal lobes is not followed by any definite physiological results. The animals retain their appetites and instincts, and are capable of exhibiting emotional feeling. The sensory faculties—sight, hearing, touch, taste, and smell—remain unimpaired. The powers of voluntary motion are retained in their integrity, and there is little to indicate the presence of such an extensive lesion or a removal of so large a part of the brain. And yet, notwithstanding this apparent absence of physiological symptoms, I could perceive a very decided alteration in the animal's character and behaviour, though it is difficult to state in precise terms the nature of the change. The animals operated on were selected on account of their intelligent character. After the operation, though they might seem to one who had not compared their present with the past fairly up to the average of monkey intelligence, they had undergone a considerable psychological alteration. Instead of, as before, being actively interested in their surroundings, and curiously prying into all that came within the field of their observation, they remained apathetic or dull, or dozed off to sleep, responding only to sensations or impressions of the moment, or varying their listlessness with restless and purposeless wanderings to and fro. While not actually deprived of intelligence, they had lost to all appearance the faculty of attentive and intelligent observation" (*Functions of the Brain*, 1st ed., p. 231).

Thus the frontal lobes appear to have to do with cognition and intellectual action. If so, the grey matter on the surface of the brain may be mapped out into three great areas—an area concerned in cognitions and volitions in front, a motor or ideo-motor area in the middle, and a sensory area behind. These distinctions are no doubt arbitrary to a considerable extent; but, if they are retained as the expressions of a working hypothesis, they are of service. Long ago, and prior to the researches above alluded to, Dr Hughlings Jackson pointed out that disease of certain areas of grey matter on the cortex of the hemispheres may occasion epileptiform convulsions, localized to particular groups of muscles. The theory of the localization of motor functions has been of great service in the diagnosis and prognosis of such diseases. As to the localization of the faculty of language in the third left frontal convolution, founded on pathological evidence, see APHASIA, vol. ii. p. 171.

Consciousness.

The functions of the nervous system have now been described; but they are so complicated and so closely related to each other as to make it no easy matter to form a conception of the system working as a whole. The progress of discovery naturally tends to differentiation, and probably to attach too much importance to one organ as compared with the others, so that we are in danger of losing sight of the solidarity of the whole nervous system. Probably every nervous action, however minute and evanescent, affects more or less the entire system, and thus there may be an under-current of nervous action streaming into and out of the nerve-centres, along with a perpetual series of interactions in the centres themselves, contributing to and accounting for the apparent continuity of conscious experience. Certain relations of one nerve-centre to the others are indicated in fig. 31. No one now doubts that consciousness has an anatomical substratum, but the great problem of the relation between the two is as far from solution as in the days when little or nothing was known of the physiology of the nervous system. Consciousness has been driven step by step upwards until now it takes refuge in a few thousand nerve-cells in a portion of the grey matter of the cortex of the brain. The ancients believed that the body participated in the feelings of the mind, and that, in a real sense, the heart might be torn by contending emotions. As science advanced, consciousness took refuge in the brain, first in the medulla and lastly in the cortex. But even supposing we are ultimately able to understand all the phenomena—chemical, physical, physiological—of this intricate ganglionic mechanism we shall be no nearer a solution of the problem of the connexion between the objective and subjective aspects of the phenomena. It is no solution to resolve a statement of the phenomena into mental terms or expressions and to be content with pure idealism; nor is it any better to resolve all the phenomena of mind into terms describing physical conditions, as in pure materialism. A philosophy that recognizes both sets of phenomena, mutually adjusted and ever interacting, may be no explanation; but at all events it is unpretentious, recognizes facts, and does not delude the mind by offering a solution which is no solution at all. But apart from the ultimate question there is the important one of whether physiologists are on the whole right in relegating sensation or consciousness entirely to the grey matter of the brain. The facts of comparative physiology are against such an exclusive notion, because we cannot deny consciousness to many animals having rudimentary nervous systems. As already said, research in anatomy and physiology and the observation of disease have driven physiologists to adopt the view that the brain is the organ of sensation. This is no doubt true in the sense that it ultimately receives all those nervous impressions that result in consciousness; but the parts transmitting the nervous impressions are in another sense as much concerned in the production of conscious states as the brain. This view of the matter, put forward by Professor John Cleland in 1870, has not received from psychologists the attention it deserves. His thesis is—

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[1] For figures of human brain showing motor areas, see Foster's *Physiology*, 4th ed., figs. 86 and 87, pp. 627, 628.

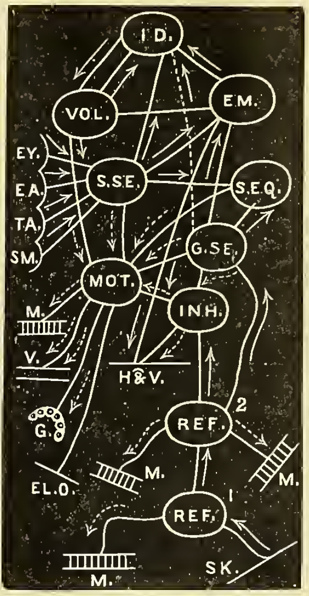

Fig. 31.—*M.*, muscle; *SK.*, skin; *REF.*, reflex centre; *INH.*, inhibitory centre; *MOT.*, motor centre; *G.SE.*, centre of general sensation; *S.SE.*, centre of special sensation; *S.EQ.*, sense of equilibrium; *VOL.*, volitional centre; *EM.*, emotional centre; *ID.*, ideational centre; *EY.*, eye; *EA.*, ear; *TA.*, taste; *SM.*, smell; *V.*, vessel; *G.*, gland; *H&V.*, heart and vessels; *EL.O.*, electric organs in some fishes. The arrows indicate direction of currents, by following which the influence of one centre over another may be studied.

> "that the consciousness extends from its special seat so far as there is continuity of the impressed condition; that when an irritation is applied to a nerve-extremity in a finger or elsewhere the impression (or rather impressed condition) travels, as is generally understood, but exists for at least a moment along the whole length of the nerve, and that as soon as there is continuity of the impressed condition from finger to brain the consciousness is in connexion with the nerve and is directly aware of the irritation at the nerve-extremity" (*Evolution, Expression, and Sensation*, Glasgow, 1881, p. 106).

This view is quite consistent with all the facts of nervous physiology and presents fewer difficulties than the one generally held, which drives consciousness into the recesses of the nerve-cells in the cortex of the cerebral hemispheres. It appears to keep clear of the prevailing error in the philosophy of modern physiology,—that of regarding the body and even the nervous system as a vast series of almost independent organs, losing sight of the community of function and interdependence of parts, characteristic of the body of one of the higher animals.

CIRCULATION IN THE BRAIN.

Circulation in brain.

A due supply of healthy arterial blood and the removal of venous blood are essential to cerebral activity. The brain is contained in an osseous case of which the total capacity is variable. The cerebral substance undergoes almost insignificant changes of volume even under a pressure of 180 mm. of mercury. The quantity of blood in the cranium may vary. In the rabbit not more than 1 per cent. of the total quantity of blood of the body (equal to about 5 per cent. of the total weight of the organ) is present at any one time in the brain, whereas in the kidney, by weight, the blood may amount to nearly 12 per cent., and in the liver to as much as nearly 30 per cent. (Foster). If a small round window be made in the cranium and a suitable piece of glass fitted into it, the veins of the pia mater may be observed to dilate or contract if intermediate pressure be made on the veins of the neck. There is evidently, then, within the cranium some arrangement by which such variations become possible. This is probably accomplished by the anatomical arrangements of the sub-arachnoid spaces. These spaces, containing fluid, communicate freely with each other and with the space surrounding the spinal cord, so that when the quantity of blood increases in the cranium a corresponding quantity of fluid escapes into the spinal space, the walls of which are not inextensible like those of the cranium. In young children, before the fontanelles are closed, the variations of circulation and blood-pressure cause pulsations, of which there are two kinds—those coinciding with the ventricular systole, produced by the pulsation of the arteries at the base of the brain, and those coinciding with expiration. Pressure on the brain-substance beyond a limit leads to paralysis, unconsciousness, and death. The large sinuses probably assist in equalizing internal pressure, and, as inspiration favours the flow of blood from the sinuses, too great distension of these is also avoided. Vaso-motor nerves regulate the calibre of the arterioles of the brain, but we know nothing of the conditions affecting the nerves. Nor do we know how the waste-products of the brain are got rid of. There are no lymphatic vessels, but there are spaces around many of the vessels. These probably communicate with the cavities in the membrane containing the cerebro-spinal fluid, the value of which, as suggested by Foster, "depends in all probability more on its physiological properties as lymph than on its mechanical properties as a mere fluid." The grey matter is much more richly supplied with capillaries than the white matter, as seen in fig. 32.

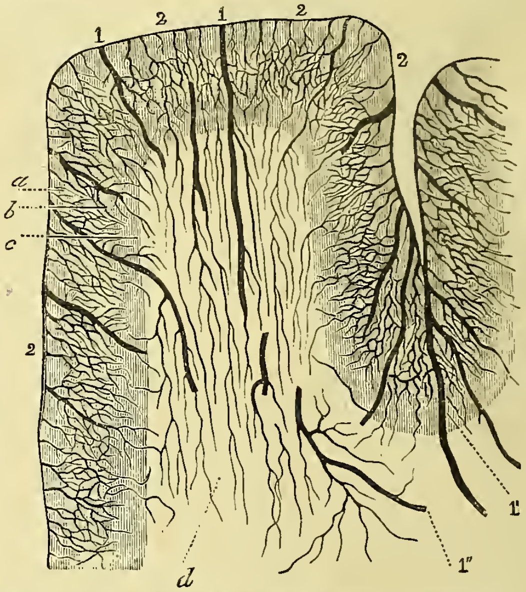

Fig. 32.—Injected convolution of cerebrum (Duret). 1, 1, medullary arteries; 1′, group of medullary arteries in fissure between two neighbouring convolutions; 1″, arteries of system of arcuate fibres; 2, 2, 2, arteries of grey substance of cortex; *a*, large-meshed capillary network situated under pia mater; *b*, smaller-meshed capillary network situated in middle layers of cortex; *c*, somewhat larger network in internal layers adjoining white substance; *d*, capillary network of white substance.

CRANIAL NERVES.

The general anatomy of these nerves is described under ANATOMY, vol. i. p. 880 *sq.*, and it remains only to enumerate their functions. Their deep roots have also been alluded to in treating of the medulla oblongata and the pons Varolii above.

Cranial nerves.

1. The *olfactory nerve*. The nerve of smell (see SMELL).
2. The *optic nerve*. The nerve of sight (see EYE).
3. The *oculo-motor* or *third nerve*,—motor, supplying all the muscles of the eyeball except the superior oblique and external rectus; it also supplies the circular fibres of the iris and the ciliary muscle (see EYE).
4. The *pathetic* or *fourth nerve*,—motor, supplying the superior oblique muscle.
5. The *trigeminal* or *fifth nerve*. It has three branches: (A) The *ophthalmic* division of the fifth, or nerve of Willis, is sensory and supplies (*a*) the skin of the forehead, the eyebrow, the upper eyelid, the root and lobule of the nose; (*b*) the palpebral and ocular conjunctiva, the mucous membrane of the lacrymal passages, the frontal sinuses, the upper part of the nasal mucous membrane; (*c*) the cornea, the iris, the choroid, and the sclerotic; (*d*) the periosteum and bones of the frontal, orbital, and nasal regions; and (*e*) muscular sensibility to the intra-orbital muscles. It also influences the secretion of the lacrymal gland. It contains the fibres from the sympathetic governing the radiating fibres of the iris (see EYE), and also the vaso-motor fibres for the iris, choroid, and retina. It is associated with the otic ganglion. (B) The *superior maxillary* division of the fifth furnishes sensory branches to (*a*) the skin of the lower eyelid, alæ of the nose, upper lip, and skin covering the malar bone; (*b*) the mucous membrane of the nasal, pharyngeal, and palatine regions, the maxillary sinuses, the gums, the upper lip, and the Eustachian tube; (*c*) the periosteum of the bones corresponding to its distribution; and (*d*) the teeth of the upper jaw. It furnishes filaments to the nasal and palatine glands, and prob-

ably to the glands of the velum palati. It contains vaso-motor fibres from the sympathetic for the vessels, and is associated with the spheno-palatine ganglion. (C) The *inferior maxillary* division of the fifth contains sensory branches to (*a*) the skin of the cheeks, temples, lower lip, chin, front part of the ear, and external auditory canal; (*b*) the mucous membrane of the cheeks, lips, gums, front part of the tongue, the mucous membrane of the tympanum, and the mastoid cells; (*c*) the periosteum of the lower jaw and temporal bones; (*d*) the teeth of the lower jaw; (*e*) the temporo-maxillary articulation; and (*f*) the muscles in the neighbourhood (muscular sensibility). It thus exercises an influence on taste, hearing, and secretion (see NUTRITION). It contains vaso-motor fibres for the blood-vessels. Its motor branch is distributed to the muscles of mastication; and it is related to two ganglia, the otic and the sub-maxillary.

6. The *sixth nerve* is motor, and supplies the external rectus muscle of the eyeball only.

7. The *facial* or *seventh nerve* is purely motor, and supplies all the muscles of expression. It also contains secretory fibres influencing the action of the salivary glands (see NUTRITION). Some assert that the chorda tympani contains gustatory fibres, but the question has not been settled. Claude Bernard found that the facial contains vaso-motor fibres.

8. The *auditory* or *eighth nerve* is the nerve of hearing (see EAR). In addition to purely auditory filaments it contains fibres from the semicircular canals having to do with impressions of movement in space (see pp. 38, 39).

9. The *glosso-pharyngeal nerve* is sensory to (*a*) the mucous membrane of the posterior part of the tongue (nerve of taste), the pillars of the fauces, the anterior face of the epiglottis, and the tonsils; and (*b*) the mucous membrane of the tympanum, the fenestra ovalis and fenestra rotunda (see EAR), the mastoid cells, and the Eustachian tube along with the fifth. It probably supplies motor fibres to the muscles of the pharynx, but this is doubtful. Vulpian states that it contains vaso-dilator fibres for the vessels of the posterior third of the tongue.

10. The *pneumogastric* or *vagus nerve* has many complicated actions. (A) It is sensitive to (*a*) the mucous membrane of all the respiratory passages, including specially the larynx; (*b*) the heart; (*c*) a portion of the digestive tube, namely, the base of the tongue, the velum palati, the pharynx, œsophagus, stomach, and probably the duodenum; (*d*) it confers muscular sensibility on the muscles to which it is distributed; (*e*) the mucous membrane of the biliary passages; (*f*) a part of the dura mater corresponding to the transverse and occipital sinuses; (*g*) the posterior part of the auditory canal. By the laryngeal branches it specially stimulates expiratory movements. (B) It is motor to (*a*) many of the muscles of the palate; (*b*) the constrictors of the pharynx; (*c*) the œsophagus; (*d*) the larynx by (*α*) the superior laryngeal to the crico-thyroid muscle and a portion of the arytenoid, and by (*β*) the inferior or recurrent laryngeal to the rest of the muscles of the larynx; and (*e*) to the muscular fibres of the bronchial tubes. (C) It contains vaso-inhibitory fibres for the heart. In connexion with this organ the vagus also contains sensory fibres and fibres belonging to the depressor system. (D) It influences secretion in the stomach (see NUTRITION); but it is doubtful whether it has any action on the renal secretion. (E) It influences the production of glycogen in the liver (see NUTRITION).

11. The *spinal accessory* is a motor nerve supplying the sterno-cleido-mastoid muscle and the trapezius. It gives an important branch to the vagus (*internal* branch), which supplies all the motor fibres in that nerve distributed to the larynx, except those in the superior laryngeal supplying the crico-thyroid muscle, and also the motor fibres of the vagus sent to the pharynx. According to Heidenhain, it also supplies the vagus with the inhibitory cardiac fibres.

12. The *hypoglossal* is exclusively a motor nerve supplying the muscles of the tongue and also the sub-hyoid muscles (see ANATOMY). It also contains vaso-motor filaments.

SPINAL NERVES.

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The spinal cord gives origin in its course to thirty-one pairs of spinal nerves, each nerve having two roots, anterior and posterior, the latter being distinguished by its greater thickness and by the presence of an enlargement called a ganglion, in which are found numerous bi-polar cells. The anterior root is motor, the posterior sensory. The mixed nerve after junction of the roots contains (*a*) sensory fibres passing to the posterior roots; (*b*) motor fibres coming from the anterior roots; (*e*) sympathetic fibres, either vaso-motor or vaso-dilator.

SYMPATHETIC SYSTEM.

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The fibres of the sympathetic system consist of two kinds—(1) of grey or gelatinous fibres, destitute of the white substance of Schwann; and (2) of medullated fibres similar to those met with in the cerebro-spinal centres. The grey fibres originate in the ganglia so prevalent in the sympathetic system, whilst the medullated fibres are believed to come from the cerebro-spinal system. The trunk of the great sympathetic nerve consists of a chain of swellings or ganglia, connected by intermediate cords of grey nerve-fibres, and extending nearly symmetrically on each side of the vertebral column, from the base of the cranium to the coccyx. On this part of the nerve twenty-four ganglia are placed on each side. This great trunk, as it passes along the spine, is connected with the spinal nerves, the connecting fibres being of the two kinds already described. The grey fibres dominate in the sympathetic nerves, and the medullated in the cerebro-spinal; and these two elements are mixed in various proportions in both of the great divisions of the nervous system. At their lower extremities the main trunks of opposite sides generally unite in the middle line; and at the upper ends each trunk, after being connected with the eighth and ninth cranial nerves, extends to the cranium, passes into that cavity along with the internal carotid artery, and there, as well as in other situations, comes into connexion with all the remaining cranial nerves, except the olfactory, auditory, and optic. This conjunction may be effected directly, as with the fourth, sixth, and ninth nerves; or through a ganglion, as the ophthalmic, with the third and fifth; the spheno-palatine, otic, and sub-maxillary, with the fifth and seventh, or facial; the geniculate, with the seventh or facial; the jugular, with the glosso-pharyngeal; and with the vagus, through one of its own ganglia. On the fibres of the sympathetic distributed to the viscera numerous ganglia, or plexuses in which ganglia exist, are met with, and frequently there is a plexus following the course of each vessel.

Functions of sympathetic.

As to the functions of the sympathetic, experiment has led to the following conclusions.

(*a.*) The *vaso-motor fibres of the head* are supplied by the cervical portion of the sympathetic, and originate in the cervical region of the cord, proceeding from it by the anterior roots of the lower cervical and upper dorsal nerves. The fibres supplying the radiating fibres of the iris also come from that region (see EYE).

(*b.*) The *vaso-motors of the upper limbs* and of the thorax come (*α*) from the inferior cervical and superior thoracic ganglia, and (*β*) from the cord, by communicating branches between the third and seventh dorsal vertebræ.

(*c.*) The *vaso-motor fibres of the lower limbs* come from the cord through the sciatic and crural nerves, whilst those of the pelvic organs are derived from the abdominal ganglia of the sympathetic.

(*d.*) The *vaso-motors of the abdominal viscera* exist chiefly in the splanchnic nerves; some fibres supplying the stomach appear to be derived from the pneumogastric.

(*e.*) The *splanchnic nerves* all arise in man from the thoracic ganglia of the sympathetic—the greater splanchnic from the fifth to the tenth ganglia, the lesser splanchnic from the tenth and eleventh, and the smallest splanchnic from the twelfth ganglion. The splanchnics supply the stomach, liver, spleen, pancreas, intestines, and kidneys. Division causes dilatation of vessels; irritation causes contraction of vessels, and appears also to arrest or inhibit peristaltic motions of the stomach and intestines. Probably they also contain secretory filaments. The functions of vaso-motor nerves have been already described.

A very complete bibliography of works relating to the nervous system will be found in the *Dictionnaire Encyclopédique des Sciences Médicales*, 2d ser., xii. p. 619. For the comparative anatomy of invertebrates consult Gegenbauer, *Elements of Comparative Anatomy* (trans. and rev. by F. Jeffrey Bell and E. Ray Lankester, London, 1878); for the comparative anatomy of vertebrates, Owen, *Anatomy of Vertebrates* (3 vols., London, 1866); for details in human anatomy, Quain, *Elements of Anatomy* (9th ed., ed. by Allen Thomson, E. A. Schäfer, and G. D. Thane, London, 1882); for general physiology, Foster, *Text-Book of Physiology* (4th ed., London, 1883); for special details in physiology, H. Beaunis, *Nouveaux Éléments de Physiologie Humaine* (2d ed., Paris, 1881); (specially for the functions of the cranial nerves) Flint, *Physiology of Man* (vol. v., New York, 1872); Ferrier, *On the Functions of the Brain* (London, 1876, also new ed.); Meynert, "On the Brain of Mammals," in Stricker's *Manual of Human and Comparative Histology* (vol. ii., the New Syd. Soc., London, 1872); Flechsig, *Die Leitungsbahnen im Gehirn und Rückenmark des Menschen* (Leipsic, 1876), also "Zur Anatomie und Entwickelungsgeschichte der Leitungsbahnen im Grosshirn des Menschen," in Du Bois-Reymond's *Archiv für Anatomie* (Leipsic, 1881); Gudden, "Experimentaluntersuchungen über das peripherische und centrale Nervensystem," in *Arch. f. Psychiatrie* (vol. ii., 1869, p. 713); Hitzig, *Untersuchungen über das Gehirn* (new series, 1874); Goltz, "Ueber die Verrichtungen des Grosshirns," in Pflüger's *Archiv* (1876), also "The discussion on the localization of function in the cortex cerebri," in *Trans. of Inter. Med. Cong.* (vol. i., 1881, p. 218); Munk, *Ueber die Functionen der Grosshirnrinde* (Berlin, 1881); Ross, *Treatise on the Diseases of the Nervous System* (2d ed., London, 1883).

(J. G. M.)

PART III.—PHYSIOLOGY OF PLANTS.

THE body of a plant, like that of an animal, consists of one or more structural units which are termed "cells," and in plants, as in animals, the cell consists essentially of an individualized mass of protoplasm.

The probable structure and chemical composition of protoplasm have been already considered. It need only be stated here that the protoplasmic cell-contents do not consist of pure protoplasm, but that the protoplasm contains imbedded in it particles of various substances which may be of the nature of food, or which may have been formed from food, or which are products of the metabolism of protoplasm; it is to the presence of these particles that the granular appearance of protoplasm is largely due. Moreover, there is present in the protoplasm of the cell, in the vast majority of cases at least, a well-defined, highly-refractive, usually somewhat spherical body, also protoplasmic in nature, the nucleus.

Cell-walls.

The cell or cells constituting the body of a plant present, in most cases, the important peculiarity that the protoplasm is enclosed in a membrane termed the "cell-wall." This membrane does not consist of protoplasm, but of a substance, cellulose, belonging to the group of the carbohydrates, and having the formula $x\mathrm{C}_6\mathrm{H}_{10}\mathrm{O}_5$. All cell-walls do not, however, consist exclusively of this sub-